OUT-MIGRATION DYNAMICS OF JUVENILE ADFLUVIAL BULL TROUT IN TRIBUTARIES TO THE LOWER CLARK FORK RIVER, MONTANA

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2021

ACKNOWLEDGEMENTS

Funding for this study was provided by Avista through the Clark Fork Settlement Agreement. I thank my advisor, Dr. Christopher Guy, for his guidance, support, and encouragement every step of the way. I also thank my committee members, Eric Oldenburg, and Dr. Thomas McMahon, for their support and guidance. Thank you to everyone from Avista; Montana Fish, Wildlife and Parks; U.S. Fish and Wildlife Service; and Idaho Fish and Game for their input and review of the study. Thanks to Dylan Gollen, Josh Storaasli, Kristin Lantz, and Ciera Pitts for their hard work in the field and lab. Thank you to Brice Adams and others at the Abernathy Fish Technology Center for processing genetic samples. I also thank my husband Matthew Bregartner for his support and encouragement.

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ABSTRACT

In the lower Clark Fork River, Montana, a two-way trap-and-haul program is implemented to conserve the adfluvial life-history strategy in Bull Trout *Salvelinus confluentus* populations in the presence of hydropower dams. We used the infrastructure in place for the program, including a permanent weir trap and multiple stationary PIT antennas, to evaluate the demographic characteristics and out-migration dynamics of juvenile bull trout, and assess the efficacy of the downstream trapping component of the trap-and-haul program. We PIT-tagged 821 juvenile Bull Trout in Graves Creek, and 144 Bull Trout in East Fork Bull River in the summer of 2019 and summer of 2020. Bull Trout in Graves Creek were primarily age 1 and age 2, with a small number of age-3 Bull Trout present (< 1%). In East Fork Bull River, age-3 Bull Trout represented 14% – 46% of the population, with a small number of age-4 and older Bull Trout present (4% – 6%). From July 2019 through December 2020, 308 tagged Bull Trout out-migrated from Graves Creek, and most out-migrants were age 2 (n = 221). In East Fork Bull River, 18 Bull Trout out-migrated, and most out-migrants were age 3 (n = 13). Capture efficiency of the permanent weir in Graves Creek varied from 83% to 100% in autumn 2019 and 2020 and was substantially lower in the spring (14%). The majority of Bull Trout out-migrated from Graves Creek during autumn 2019, spring 2020, or autumn 2020 trapping seasons (n = 276). In Graves Creek, the largest Bull Trout within the 2018 year-class were five times more likely to out-migrate at age 1 when compared to smaller fish within the cohort. The magnitude of age-1 out-migration was positively related to density. Relative changes in abiotic factors, including discharge, water temperature, and photoperiod, were cues to out-migration, and the direction of change varied by season. Understanding the demographic characteristics and out-migration dynamics of the Bull Trout in Graves Creek and East Fork Bull River enables more informed management of the trap-and-haul program and can be used to inform conservation efforts of other migratory Bull Trout populations.

CHAPTER ONE

DEMOGRAPHIC CHARACTERISTICS AND DISTRIBUTION OF JUVENILE ADFLUVIAL BULL TROUT AT THE TRIBUTARY SCALE

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Manuscript Information

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Transactions of the American Fisheries Society

Status of Manuscript:

__x__ Prepared for submission to a peer-reviewed journal

____ Officially submitted to a peer-reviewed journal

____ Accepted by a peer-reviewed journal

____ Published in a peer-reviewed journal

Abstract

Conservation efforts for Bull Trout *Salvelinus confluentus* are increasingly focused at the tributary-scale due to habitat fragmentation from physical and thermal barriers. We assessed the demographic characteristics and the distribution of juvenile Bull Trout in relation to water temperature, in Graves Creek and East Fork Bull River, two tributaries to the lower Clark Fork River that are currently undergoing active management to conserve adfluvial Bull Trout. In Graves Creek, a small (< 5.2 km) tributary with a high-density of juvenile Bull Trout, age-1 Bull Trout represented the majority of the population, followed by age-2 Bull Trout, with few age-3 Bull Trout present (< 1%). In East Fork Bull River, with double the length of stream accessible and lower density when compared to Graves Creek, the age-class structure was older, with age-3 Bull Trout representing 14% – 46% of the population, and a small number of age-4 and older Bull Trout present (4% – 6%). The majority of Bull Trout out-migrated from Graves Creek at age 2, and from East Fork Bull River at age 3. The sex ratio of juvenile Bull Trout in both tributaries were similar, in Graves Creek juvenile Bull Trout were 52% female and 48% male, and in East Fork Bull River, juvenile Bull Trout were 48% female and 52% male. Water temperature metrics consistently explained variation in density of juvenile Bull Trout within each tributary, and the lowest elevation and warmest reaches contained the lowest densities of Bull Trout; however, the highest elevation and coldest reaches did not consistently contain the highest densities of Bull Trout. Information on the demographic characteristics and distribution of juvenile adfluvial Bull Trout in Graves Creek and East Fork Bull River may be used to identify life-history strategies in other populations and prioritize conservation actions.

Introduction

Anthropogenic disturbances and introduction of non-native species have led to general declines in Bull Trout populations across their native range (Rieman et al. 1997; USFWS 2015a); thus, Bull Trout were listed as threatened under the Endangered Species Act in 1999 (USFWS 1999). Bull Trout demonstrate plasticity in life-history strategies (Rieman and Mclntyre 1993; Zymonas 2006). Life-history strategies of Bull Trout can vary among and within populations, but are generally classified as either resident (i.e., remain in the same stream throughout their life) or migratory (i.e., leave their natal stream to grow and mature in larger water bodies before returning to their natal stream to spawn). Migratory forms of Bull Trout can be fluvial (i.e., use large lotic systems to grow and mature) or adfluvial (i.e., use lentic systems to grow and mature) (Rieman and Mclntyre 1993). Variation in life-history strategies can increase the resiliency of salmonid populations and is vital to the long-term persistence of a species (Rieman and Mclntyre 1993; Rieman and Allendorf 2001; Hilborn et al. 2003; Morita et al. 2009; Schindler et al. 2010; Moore et al. 2014). Conserving diversity in life-history strategies of Bull Trout is considered a primary goal of the Bull Trout recovery plan developed by the United States Fish and Wildlife Service (USFWS 2015b).

Bull Trout use a variety of habitat types throughout their life cycle because of their diverse life-history strategies (Rieman and Mclntyre 1993). Widespread habitat fragmentation has reduced connectivity among habitats and restricted the range of many Bull Trout populations (Rieman et al. 1997; Rieman and Allendorf 2001). Regardless of life-history strategy, all Bull Trout use headwater tributaries for spawning and rearing (Rieman and Mclntyre 1993). As fragmentation of habitat occurs, Bull Trout populations often become restricted to headwater tributaries and reliant on resident reproduction. In some areas, tributary populations of resident fish represent the last remnants of formerly wide-spread Bull Trout populations (Nelson et al. 2002; Rieman et al. 1997b).

In populations fragmented by physical barriers, management actions such as trap-and-haul programs may be necessary to restore and maintain the migratory life-history strategy. Trap-and-haul programs entail capturing fish upstream, downstream, or both of a barrier and physically transporting the fish around one or multiple barriers. Trap-and-haul programs are resource intensive and require a high degree of human intervention (Kock et al. 2020). Thus, it is vital that biologists are able to identify life-history strategies currently present at the tributary scale and identify the steps necessary to reestablish the migratory life-history strategy in resident populations. Identifying the life-history strategies present in Bull Trout populations at the tributary scale can be challenging given that multiple life-history strategies may be present, and demographics may vary among and within each life-history strategy (Mogen and Kaeding 2005; Zymonas 2006; Al-Chokhachy and Budy 2008). The life-history strategies present in Bull Trout populations have implications for the demographic structure of the population (Mogen and Kaeding 2005; Zymonas 2006; Al-Chokhachy and Budy 2008). Understanding the demographic structure associated with migratory populations can guide efforts to restore the migratory life-history strategy in populations where the migratory life-history strategy has declined or been eliminated.

Thermal barriers resulting from increasing water temperatures due to climate change will continue to fragment migratory Bull Trout populations, and further the reliance of Bull Trout populations on headwater tributaries to persist (Rieman et al. 2007; Isaak et al. 2015). The distribution of juvenile Bull Trout has been found to be positively correlated with increasing elevation and decreasing water temperatures (Dunham and Rieman 1999; Paul and Post 2001; Dunham et al. 2003); however, much of this work has occurred at the watershed or larger scale, and focused on the probability of Bull Trout being present or absent in a stream or reach. The ability to predict presence of Bull Trout and use occupancy models to anticipate responses to future changes are valuable tools to prioritize conservation efforts to focus on tributaries likely to support Bull Trout in the future (Isaak et al. 2015). However, within headwater tributaries, thermal conditions can vary considerably, even at fine spatial scales (< 1 km), and the variability can influence the distribution of thermally sensitive species (Leach et al. 2016). As conservation efforts for Bull Trout focus on the tributary scale, and may require an increased level of intervention and resources, it will be vital to understand the role that temperature has on the density and distribution of juvenile Bull Trout within tributaries. The relationship between water temperature and density of Bull Trout within streams has implications for the potential consequences of non-native species interactions (McMahon et al. 2007), and for the anticipated effects of climate change (Rieman et al. 2007; Isaak et al. 2015). Additionally, understanding how variability in water temperature conditions influences Bull Trout distributions will allow for the prioritization of reaches within tributaries for conservation.

For this study, we focused on two tributaries to the lower Clark Fork River, Montana, Graves Creek and the East Fork Bull River. A trap-and-haul program is implemented on Graves Creek and East Fork Bull River to conserve the adfluvial migratory life-history component in the populations (DeHaan and Bernall 2013). The infrastructure in both tributaries as a result of the trap-and-haul program offers an opportunity to gain understanding of the demographic structure and distribution of juvenile Bull Trout with a known life-history strategy, and to observe the demographic characteristics of populations currently undergoing active management to conserve migratory Bull Trout. We sought to answer the following questions: 1) what is the age structure, length-at-age, and age-at-out-migration for juvenile adfluvial Bull Trout in Graves Creek and East Fork Bull River, and does this vary between streams and within streams between years; 2) what is the sex ratio of juvenile migratory Bull Trout in tributaries; 3) what is the sex ratio of out-migrating Bull Trout; and 4) does density of juvenile Bull Trout vary spatially within tributaries and is the variation related to water temperature?

Study Site

The Clark Fork River flows in a northwest direction across western Montana before reaching Lake Pend Oreille in Idaho. The lower Clark Fork River is characterized by a series of hydroelectric dams and reservoirs. From 1913 to 1959, three hydropower dams were constructed on the lower Clark Fork River with no fish passage facilities. The downstream most dam, Cabinet Gorge Dam, is located in Idaho approximately 16 km upstream from confluence of the Clark Fork River with Lake Pend Oreille. Cabinet Gorge Reservoir spans approximately 32 km upstream, to Noxon Rapids Dam. Noxon Reservoir spans for 60 km upstream from Noxon Rapids Dam to Thompson Falls Dam. A two-way trap-and-haul program is implemented to maintain and conserve the adfluvial life-history strategy in Bull Trout populations in the lower Clark Fork River. For the trap-and-haul program, juvenile Bull Trout are captured out-migrating from their natal streams and transported directly to Lake Pend Oreille. Adult Bull Trout are captured at the base of Cabinet Gorge Dam and transported upstream to their most likely region of origin, to allow them access to their natal streams to spawn (Dehaan et al. 2011). Graves

Creek and the East Fork Bull River are two of the primary streams in the trap-and-haul program and have confirmed populations of adfluvial Bull Trout (DeHaan and Bernall 2013).

Graves Creek enters the north side of Noxon Reservoir as a fourth order stream with a length of approximately 21 km (Figure 1.1). Graves Creek Falls is a natural barrier to upstream fish passage located at river kilometer 5.2, and Bull Trout distribution is limited to the reach downstream of the falls (Figure 1.1). Bull Trout and Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi,* are the most predominant species present below Graves Creek Falls. Low densities of Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, Rainbow Trout *Oncorhynchus mykiss*, and Mountain Whitefish *Prosopium williamsoni* occur below Graves Creek Falls (Horn and Tholl 2011). The habitat in Graves Creek below Graves Creek Falls is primarily classified as pool-riffle stream type, with small sections of higher gradient step-pools (River Design Group Inc 2005). Public land encompasses Graves Creek from Graves Creek Falls to around the top of reach 6 (Figure 1.1), at which point land ownership transitions to entirely private land (Figure 1.1) (River Design Group Inc 2005). Throughout the sampling area of the study, past and current land-use, road encroachment, and riparian harvesting influence the habitat characteristics of Graves Creek, in the public and privately owned sections (River Design Group Inc 2005). From 2002 through 2012, juvenile Bull Trout in Graves Creek were captured for the trap-and-haul program using screw traps and temporary weir traps. In 2012, a permanent, concrete bedded weir trap was constructed in Graves Creek, and operation of the permanent weir began in 2013. A permanent PIT-monitoring station is also present, with two antennas located upstream of the weir, two integrated into the weir, and two antennas downstream of the weir (Figure 1.1).

East Fork Bull River is approximately 13-km long and enters the Bull River, a tributary to Cabinet Gorge Reservoir, as a fourth order stream (Figure 1.2). Near the confluence with the Bull River, the East Fork Bull River splits into a north channel and a south channel, which remain separated at the confluence with the Bull River (Figure 1.2). The species assemblage in East Fork Bull River varies longitudinally. The upper reaches are primarily inhabited by Bull Trout and Westslope Cutthroat Trout. The lower reaches of East Fork Bull River are inhabited by Bull Trout, Westslope Cutthroat Trout, and non-native species, including Rainbow Trout, Brown Trout, and Brook Trout (Horn and Tholl 2011). The upper reaches of East Fork Bull River are primarily step-pool habitat, transitioning to a braided habitat type in the lower reaches (Land and Water Consulting Inc 2001). The East Fork Bull River primarily flows through public land, with a small portion of private land ownership in the lower reaches (Land and Water Consulting Inc 2001). In the lowermost reaches of East Fork Bull River (below reach 3), there is extensive evidence of past land-use practices such as logging and modifications for irrigation that simplified the habitat and increased the width of the stream (Land and Water Consulting Inc, 2001). Habitat becomes more complex further upstream as riparian conditions transition to dense old growth cedar (Land and Water Consulting Inc, 2001). Temporary weirs and screw traps were operated in the lower East Fork Bull River to capture out-migrating juvenile Bull Trout for the transport program (Figure 1.2). Two screw traps were operated in the south channel of East Fork Bull River, and temporary weirs were operated in both channels when conditions allow. Screw traps were used when discharge and debris cause the weirs to be non-functional (generally early April through late June).

Methods

Sampling

Sampling reaches were selected on each stream using a stratified random sampling design. In Graves Creek, 12, 100-m reaches were selected (Figure 1.1). In East Fork Bull River, seven historic reaches (reaches sampled annually or biennially from 2002 through 2018) were selected, and an additional eight reaches were randomly selected in areas of the East Fork Bull River with historically high densities (above historic reach 4) (Figure 1.2).

A backpack electrofisher (Smith-Root, LR-24 model) was used to sample Bull Trout at each reach, during July and August in 2019 and 2020. Settings were based on water conductivity, according to Montana Fish, Wildlife and Parks protocol. Electrofishing occurred in the downstream direction to a block net, with one operator and two netters. All fish captured were placed in containers after being netted. At regular intervals throughout the reach, fish were transferred from the container into a live-car that was placed in the stream and was perforated to allow water flow. We did not attempt to capture or enumerate age 0 because age-0 Bull Trout were not fully recruited to the gear, and would not meet the minimum size requirement for PIT-tagging.

All fish sampled were measured for total length (mm), weight (g), and scanned for the presence of a PIT-tag. If a PIT-tag was not detected, Bull Trout > 100 mm received a new 12-mm full duplex PIT tag. Prior to tag insertion, Bull Trout were anesthetized with Aqui-S. A disinfected needle or Biomark MK25 injector was used to insert the PIT tag into the anterior dorsal sinus of the Bull Trout. Bull Trout were returned to live cars and once recovered, were released throughout the sampling reach. In the 2020 sampling season, a small fin clip was collected from the upper caudal fin of > 100 mm Bull Trout from Graves Creek and > 75 mm from the East Fork Bull for genetic analysis to determine sex. Fin clips were collected from different size-classes to facilitate an unrelated study.

Age structure, length at age, and age at out-migration

Scales were removed from juvenile Bull Trout to estimate age structure. Scales were removed from all sampled Bull Trout above the lateral line ventral to the leading edge of the dorsal fins using a clean knife. In the lab, scales from ten fish were randomly selected from each 10-mm length class for aging. Scales were aged individually by two readers, and photographs of the scales were acquired using a Leica microscope. Readers did not have knowledge of fish length prior to aging. When age estimates did not agree between readers, scales were aged again, and on rare occasions a third independent reader was consulted to determine the age. If an agreement could not be reached or the quality was deemed too low to accurately determine an age, the sample was excluded, and an alternate fish was randomly selected from the size class. In East Fork Bull River, Bull Trout that were estimated to exceed 4 years were pooled because accuracy of ageing from scales declines at older ages (Zymonas and McMahon 2009). The ‘FSA’ package in R (Ogle et al. 2020) was used to construct a length-at-age key. The length-at-age key was then used to assign ages to all Bull Trout sampled, following methods outlined by Isermann and Knight (2005). Year-class was also assigned based on the year that the Bull Trout emerged (i.e., the 2018-year-class is a product of redds in 2017) to enable tracking of cohorts through time. A Welch’s *t*-test was conducted in R to test for differences in interannual variation in mean length of Bull Trout by age-class (R Core Team 2020). The age of out-migrating Bull Trout was estimated based on detections of previously tagged and aged Bull Trout on PIT-antennas in Grave Creek and East Fork Bull River from summer 2019 through autumn 2020.

Sex ratios

Sex of Bull Trout sampled in the summer of 2020 in Graves Creek and East Fork Bull River was determined using genetic analysis. All individuals were genotyped following protocols outlined in Adams et al. (2020) and two genes, SRY and 18s RNA (Yano et al. 2013) were amplified to determine sex of the individual. Sex ratio of out-migrants was estimated based on Bull Trout that were sampled in the summer of 2020 and out-migrated in the autumn of 2020.

Density estimates

Abundance at each reach was estimated using a relationship derived from historic data collected from 2002 through 2018 as part of long-term monitoring in Graves Creek and East Fork Bull River. Abundance estimates from historic multi-pass depletion surveys were calculated using the Zippin K-pass removal estimate with the 'FSA' package in R (Ogle et al. 2020), and surveys with a capture probability of < 0.5 were removed to avoid bias associated with low capture probabilities (Riley and Fausch 1992). In Graves Creek, abundances in 2019 exceeded historic numbers, therefore a depletion survey was completed in the summer of 2019 in reach 6 (Figure 1.1). The abundance estimate from this survey was included in the model described below to enable use of the model at higher abundances without extrapolating. First pass capture numbers and subsequent abundance estimates for each survey were plotted, and a linear regression model was fit to the data collected on each stream. A standardized residual cut-off of ± 3 was used to eliminate outliers. The models for Graves Creek and East Fork Bull River indicated strong evidence for a relationship between the number of Bull Trout sampled on the first pass of a multi-pass depletion survey and the population estimate produced from that survey (Graves Creek: $r^2 = 0.97$, $P = < 0.0001$, β_0: -0.611, β_1: 1.249; East Fork Bull: $r^2 = 0.97$, $P < 0$

.0001, β_0: 0.640, β_1: 1.070). Thus, data from the first pass was used to predict the abundance at each reach where single-pass electrofishing was used. High and low abundance estimates were based on the 95% prediction intervals from the linear model. Density was calculated for each reach and was the quotient from abundance and wetted area of the reach.

Density of Bull Trout and water temperature

We evaluated the relationship between density of juvenile Bull Trout at each reach during summer sampling and water temperature using regression models — all analyses were performed in R (R Core Team 2020). Water temperature was selected as an independent variable because it has been identified as an important factor influencing the distribution of juvenile Bull Trout (Saffel and Scarnecchia 1995; Paul and Post 2001; Dunham et al. 2003). Elevation was included as it is commonly used as a surrogate for water temperature (Dunham and Rieman 1999). Water temperature data were collected at each reach using submersible temperature loggers (OnSet HOBO TidbiT V2), which recorded water temperature (°C) at 30-minute intervals. For each stream and year, water-temperature data were selected from 15 August through 30 September. The date range for water temperature was selected because it enabled the greatest number of reaches to be included. Reaches where water temperature loggers were not recovered and where the logger was suspected or confirmed to be out of the water were excluded. Three water temperature metrics were selected for each reach; overall mean water temperature, mean maximum daily water temperature, and the coefficient of variation for mean water temperature. Elevation of each reach was estimated using the USGS National Map (USGS 2020). Models did not include multiple independent variables due to correlation between independent variables, and to enable interpretation of the relative importance of each variable in explaining variation in density.

Each independent variable was modeled as a linear term and a second-order term based on a priori hypothesis that the relationship between Bull Trout density and water temperature and elevation may exhibit non-linear properties. If the second-order term increased the fit of the model (determined by R^2, data visualization, and residual plots), it was selected for comparison with the other models. Models for each stream and season were ranked according to Akaike's information criterion, corrected for small sample sizes (AIC_c), Akaike weights, and R^2 values. Models were plotted with the observed data and predicted fit to visualize the relationships.

Results

Age structure, length at age, and age at out-migration

In Graves Creek, 530 Bull Trout were sampled in 2019, and 376 Bull Trout were sampled in 2020 (2 Bull Trout were recaptured within the same year and were only counted once for this analysis). In 2019, the age structure of juvenile Bull Trout in Graves Creek was primarily age-1 Bull Trout, which represented 92% of the sample (Figure 1.3). Similarly, in 2020, age-1 Bull Trout represented the majority of the sample (75%); however, the proportion of age-2 Bull Trout increased from 7% in 2019 to 24% in 2020 (Figure 1.3). Age-3 Bull Trout represented 1% of the sample in both years (Figure 1.3).

In East Fork Bull River, 78 Bull Trout were sampled in 2019, and 96 Bull Trout were sampled in 2020. In East Fork Bull River in 2019, age-1 Bull Trout represented 31% of the sample, age-2 Bull Trout represented 49% of the sample, age-3 Bull Trout represented 14% of the sample, and 6% were age 4 or older (Figure 1.4). In 2020, age-1 Bull Trout represented 33%

of the sample, age-2 Bull Trout represented 18% of the sample, age-3 Bull Trout represented 46% of the sample, and age-4 and older represented 4% of the population (Figure 1.4).

Mean length at age for juvenile Bull Trout in Graves Creek varied between years. Mean length at age 1 in 2019 (mean = 111.9 mm, [95% C.I.: ± 0.4]) was 2.4 mm larger than mean length at age 1 in 2020 (mean = 109.5 mm, ± 0.4) ($t = 4.16$, df = 693.0, $P < 0.001$) (Figure 1.3). Mean length at age 2 in 2019 (mean = 174.0 mm, ± 2.0) was 24.3 mm larger than the mean length at age 2 in 2020 (mean = 149.7 mm, ± 1.0) ($t = 10.77$, df = 58.0, $P < 0.001$) (Figure 1.3). Mean length of age-3 Bull Trout did not differ between 2019 (mean = 222.0 mm, ± 5.8) and 2020 (mean = 224.3, ± 15.2) ($t = -0.14$, df = 2.6, $P = 0.89$) (Figure 1.3).

Mean length at age for juvenile Bull Trout in the East Fork Bull River also varied between years. Mean length at age 1 in 2019 (mean = 110.3 mm, (95% C.I. ± 2.4) was 25.4 mm larger than mean length at age 1 in 2020 (mean = 84.9 mm, ± 2.6) ($t = 14.2$, df = 52.9, $P < 0.0001$) (Figure 1.4). Mean length at age 2 in 2019 (mean = 125.3 mm, ± 2.6) was 13.9 mm smaller than mean length at age 2 in 2020 (mean = 139.2 mm, ± 2.5) ($t = -7.6$ df = 45.9, $P < 0.001$) (Figure 1.4). Mean length did not differ for age-3 Bull Trout between 2019 (mean = 160.7 mm, ± 10.6) and 2020 (mean = 163.3 mm, ± 3.5) ($t = -0.45$, df = 12.03 $P = 0.66$) (Figure 1.4).

The majority of juvenile Bull Trout out-migrating from Graves Creek from summer 2019 through autumn 2020 were age 2 at the time of out-migration (72%, n = 221), followed by age 1 (27%, n = 83) and age 3 (1%, n = 4). Most juvenile Bull Trout out-migrating from East Fork Bull River from summer 2019 through autumn 2020 were age 3 at the time of out-migration (72%, n = 13), followed by age 2 (17%, n = 3) and age 4 (11%, n = 2).

Sex ratios

Overall sex ratio of Bull Trout in Graves Creek was 52% female and 48% male. For the 2019 year-class of Bull Trout, the sex ratio was 122:122 (females:males), sex ratio was 53:31 for the 2018 year-class, and was 1:2 for the 2017 year-class. Sex ratio of out-migrants in Graves Creek from the 2019 year-class was 3:5 (females:males), 33:19 for out-migrants from the 2018 year-class, and the single out-migrant from the 2017 year-class was a male. Overall sex ratio of sampled Bull Trout in East Fork Bull River was 48% female and 52% male. For the 2019 year-class of Bull Trout, the sex ratio was 16:15 (females:males), sex ratio was 6:11 for the 2018 year-class, sex ratio was 23:21 for the 2017 year-class, and 1:3 for Bull Trout ≥ age 4. Sex ratio of out-migrants in East Fork Bull River from the 2017 year-class was 6:4 (females:males), and the single out-migrant from the 2018 year-class was a female.

Density

Density of juvenile Bull Trout in Graves Creek varied by reach and year (Figure 1.5). Overall, density of juvenile Bull Trout in Graves Creek was higher in 2019, with a mean density of 0.077 (95% P.I.: 0.010) number / m^2 compared to the mean density in 2020 of 0.056 (95% P.I.: 0.010) number/ m^2. Density estimates in both years were lowest in the lowest reaches, and highest in the intermediate reaches (Figure 1.5). Density estimates for juvenile Bull Trout in East Fork Bull varied by reach and year and were lower than density estimates for juvenile Bull Trout in Graves Creek (Figures 1.5 and 1.6). Overall density in East Fork Bull River was 0.009 (95% P.I.: 0.003) number/m^2 in 2019 and 0.012 (95% P.I: 0.003) in 2020 and varied by reach and year (Figure 1.6). In both summers, zero Bull trout were sampled at the lowest reach, and in 2020, zero Bull Trout were sampled at reaches 1, 2, and 4 (Figure 1.6).

Density of Bull Trout and water temperature

Water temperature varied by reach and year in Graves Creek and East Fork Bull River (Table 1.1). The difference in elevation between reaches within the tributaries was greater in East Fork Bull River (total difference of 332 m) than in Graves Creek (total difference of 126 m) (Table 1.1). Overall mean and mean maximum daily water temperatures were higher in East Fork Bull River than in Graves Creek in both summers (Table 1.1). The range in mean water temperature in Graves Creek was 1.2 °C in 2019 and 0.9 °C in 2020 (Table 1.1). The range in mean maximum daily water temperature in Graves Creek was 2.4 °C in 2019 and 1.7 °C in 2020 (Table 1.1). The range in mean water temperature in East Fork Bull River was 1.8 °C in 2019 and 1.6 °C in 2020 (Table 1.1). The range in mean maximum daily water temperature in East Fork Bull River was 2.8 °C in 2019 and 2.6 °C in 2020 (Table 1.1).

In Graves Creek in the summer of 2019, the top ranked model (based on AIC_c score and Akaike weights) included elevation with a second order term and explained 74% of the variation in density among reaches (Table 1.2). Bull Trout density peaked at mid-elevations reaches before declining (Figure 1.7). Models including mean maximum daily temperature and coefficient of variation of temperature had similar AIC_c scores, while the model including mean overall water temperature was ranked last (Table 1.2). The relationship between density and maximum water temperature was curvilinear and peaked around 10.1 °C (Table 1.2, Figure 1.7). Similarly, the relationship between mean water temperature and Bull Trout density was curvilinear and peaked around 9.2 °C (Table 1.2, Figure 1.7). Density was inversely related with coefficient of variation in water temperature where more stable water temperatures had the highest density of Bull Trout (Table 1.2, Figure 1.7). The model containing coefficient of variation of mean water temperature was ranked first in Graves Creek during the summer of 2020 (Table 1.2), with density inversely related with coefficient of variation in water temperature where more stable water temperatures had the highest density of Bull Trout (Table 1.2, Figure 1.7). The AIC$_c$ scores of the next two models were similar; and the model containing mean overall water temperature was ranked last (Table 1.2). A curvilinear relationship was found between elevation and Bull Trout density, with a peak around 780 m (Table 1.2, Figure 1.7). Mean maximum daily water temperature showed a weak curvilinear relationship to density, with a peak around 10 °C (Table 1.2, Figure 1.7). Mean overall water temperature showed weak curvilinear relationship, with a peak around 8.9 °C (Table 1.2, Figure 1.7).

In East Fork Bull River during 2019, the top model included mean water temperature (Table 1.2). The relationship between Bull Trout density and mean water temperature was negative, with Bull Trout densities declining as water temperatures increased (Table 1.2, Figure 1.8). The second ranked model relationship showed a positive relationship between elevation and density, with the highest density reaches located at the highest elevations (Table 1.2, Figure 1.8). The model ranked third was an inverse relationship between mean maximum daily water temperature and density (Table 1.2, Figure 1.8). The model ranked last included coefficient of variation of water temperature, and the relationship between coefficient of variation of water temperature and density was weakly positive in 2019, although the reach with the highest variation did not have any Bull Trout present (Table 1.2, Figure 1.8). In 2020, the top three models included mean water temperature, mean maximum daily water temperature, and elevation, and all had similar AIC$_c$ scores. The relationship between mean water temperature and density was curvilinear, with a peak around 9.8 °C (Table 1.2, Figure 1.8). Density was inversely related to the mean maximum daily water temperature, with densities declining as water temperatures increased (Table 1.2, Figure 1.8). The relationship between elevation and density was curvilinear, with densities peaking at elevations around 950 m (Table 1.2, Figure 1.8). The model ranked last indicated that density was inversely related to the coefficient of variation of water temperature in 2020, with the highest densities associated with more stable water temperatures (Table 1.2, Figure 1.8).

Discussion

Although the Bull Trout populations in Graves Creek and East Fork Bull River both have adfluvial life-history strategies present, the demographic structure of juvenile Bull Trout within the tributaries varied. Length of available stream for juvenile Bull Trout in Graves Creek is limited to the lowest 5.2 km due to a natural barrier to fish passage. Length of available stream in East Fork Bull River is double the length of available stream in Graves Creek. Mean density of juvenile Bull Trout in Graves Creek was about nine times higher than the mean density of juvenile Bull Trout in East Fork Bull River in 2019, and about five times higher in 2020. Mean density of juvenile Bull Trout in Graves Creek in 2019 and 2020 exceeded mean density estimates collected in 2019 from direct tributaries to Lake Pend Oreille (Frawley et al. 2020). In Graves Creek, age structure was dominated by age-1 and age-2 Bull Trout, with few age-3 Bull Trout. Age-at-out-migration was reflective of the age structure, with most out-migration occurring at age 2. In East Fork Bull River, with a lower-density of juvenile bull trout relative to Graves Creek, age-structure and age-at-out-migration was shifted toward older fish relative to Graves Creek. In East Fork Bull River, age-3 Bull Trout were more common in the tributary when compared to Graves Creek, a small number of age-4 and older Bull Trout were sampled in the tributary, and age-3 Bull Trout represented the majority of out-migration.

In other systems with juvenile adfluvial Bull Trout, Bull Trout have been found to rear for an average of 1 - 4 years in tributaries before out-migrating (Fraley and Shepard 1989; Downs et al. 2006; Zymonas 2006; Ratliff et al. 2015). When the mean age-at-out-migration has been estimated based on captures of juvenile fish in other systems, age-2 Bull Trout generally make up the majority of out-migrants; however, when age-at-out-migration has been back calculated from returning migratory adults, the mean age-at-out-migration has been found to shift towards age 3 or older (Downs et al. 2006; Zymonas 2006). This shift in age distribution may suggest a survival advantage associated with larger size and older age-at-out-migration (Downs et al. 2006; Zymonas 2006). Optimal age-at-out-migration in Bull Trout and other salmonids is influenced by a balance of resource availability in the stream and risk of out-migration (Thorpe 1994; Paul et al. 2000; Ratliff et al. 2015). Thus, in East Fork Bull River, lower density of Bull Trout relative to Graves Creek likely explains the older age structure, as Bull Trout are able to remain in the stream longer to out-migrate at a larger size and older age.

While the general age structure and age-at-out-migration for juvenile Bull Trout in Graves Creek and East Fork Bull River are within the range of what would be expected based on other studies, the relative proportion of age-3 Bull Trout present in Graves Creek (1%) and out-migrating from Graves Creek (1%) is lower than what has been found elsewhere (Fraley and Shepard 1989; Zymonas 2006; Downs et al. 2006; Ratliff et al. 2015). Graves Creek has consistently contributed the majority of juvenile out-migrating Bull Trout for the trap-and-haul program, and the construction of a permanent weir trap in Graves Creek in 2013 increased the efficiency of the trapping and transport efforts. As a result, the number of spawning adults and redds in Graves Creek have increased, with redd counts in 2017 and 2018 being the highest counts observed in Graves Creek from 2001 to 2019 (Moran 2020). Thus, the duration of this study likely captured Graves Creek at a time where density is reaching the highest levels that have occurred in Graves Creek since the transport program was implemented. Continued monitoring at high densities is necessary to understand whether the age-structure that we observed was an initial response to high densities, and whether density-dependent processes will begin to stabilize the population structure and recruitment as has been observed in other Bull Trout populations (Johnston et al. 2007; Ratliff et al. 2015). In other Bull Trout populations, long-term monitoring has enabled natural resource agencies to identify the number of spawning adults necessary to maximize recruitment from tributaries before density-dependent compensatory mortality occurs (Johnston et al. 2007; Ratliff et al. 2015). Long-term monitoring of the Bull Trout population in Graves Creek could potentially enable natural resource agencies to identify the number of adult Bull Trout needed to maintain a stable population, and excess spawning adults could be translocated to other populations.

In East Fork Bull River, few Bull Trout between 250 mm – 340 mm were sampled in both years, and this length range aligns with the expected length-at-age for resident Bull Trout age 4 and older (Zymonas 2006). Genetic sex identification revealed that the largest two individuals in East Fork Bull River (> 250 mm) in 2020 were both males, which may indicate that these fish represent an alternative life-history strategy of satellite or sneaker males, that mature at a younger age and smaller size than out-migrating males and reproduce with female migratory Bull Trout. The presence of sneaker males is common in other migratory salmonids (Dodson et al. 2013) and has been found in other populations of Bull Trout (Baxter 1997). In addition to the sex of the largest fish, the proportion of age-4 and older fish (< 7%) was lower than found in other populations with mixed life-history strategies (Zymonas 2006). Thus, we did not find strong evidence that an interbreeding population of resident Bull Trout currently exists in East Fork Bull River; however, continued monitoring of the age structure and sex of the largest fish in East Fork Bull River will enable potential changes in life-history strategies to be detected. The presence of resident Bull Trout in a population is not inherently negative; however, it may be indicative of declining success of the migratory life-history strategy and increasing isolation of the population (Zymonas 2006).

Multiple interrelated factors likely contributed to the considerable interannual variation in length-at-age for juvenile Bull Trout in both tributaries. Density-dependent influences on growth are well documented for salmonids (Grossman and Simon 2020), and both intra-cohort and inter-cohort competition has been documented in other juvenile Bull Trout populations (Paul et al. 2000). Thus, varying overall densities, in conjunction with variation in year-class strength in both tributaries likely contributed to variation in length-at-age between years. Additionally, when comparing length-at-age for the juvenile component of migratory fish within tributaries, the size at which fish out-migrate can skew the mean-length-at-age found within the tributary. For example, in Graves Creek, evidence suggested that the largest fish within a cohort may be the most likely to out-migrate at age-1 (Chapter 3), however, the magnitude of this effect was controlled by density (Chapter 3). Thus, if the largest and fastest growing individuals from a year-class out-migrate at age-1, the mean length in the tributary at age-2 will likely be reduced. Additionally, the hands-on approach of trap-and-haul programs can impart variation in spawn timing of Bull Trout, potentially beyond natural levels. For example, several adult Bull Trout were captured and transported to East Fork Bull River later than average in 2018 (Moran 2020).

The considerable difference between the length-at-age for age-1 Bull Trout in East Fork Bull River in 2019 and 2020 is likely reflective of varying time of emergence. The potential interactions between density, body size and growth rate, and the magnitude of out-migration at a given age means that length-at-age in tributaries with migratory populations of Bull Trout can be influenced by several factors, and caution should be used when interpreting changes in these values. Additionally, the degree that length-at-age varied between years in both tributaries suggests that caution should be used when attempting to estimate ages of Bull Trout based only on length. Although age estimates derived from scales can be less precise than those derived from otoliths or fin rays in larger Bull Trout (> 250 mm), scales are an effective means of ageing juvenile Bull Trout < age 4 (Mogen and Kaeding 2005; Zymonas and McMahon 2009). Collecting scales from Bull Trout is non-lethal, minimally invasive, and juvenile Bull Trout scales can be mounted directly onto slides and read, thus minimizing the amount of time and resources needed for ageing in the lab. Given the value of age structure in predicting life-history strategies present in Bull Trout populations and understanding the population dynamics over time, we recommend the continued use of scales to verify age estimates in Graves Creek and East Fork Bull River, and in other populations where monitoring or conservation efforts are occurring.

Sex ratios are an important demographic parameter that can potentially be altered by anthropogenic activities (Wedekind 2012). As population sizes decline, it is increasingly important to understand the natural sex ratios of a species, and potential factors that may influence the sex ratio of a population (Wedekind 2012). Selection for or against one sex can skew sex ratios, which can ultimately increase the chance of extirpation (Wedekind 2012).

Despite the potential implications that sex ratio may have for species conservation, there is limited information available regarding the sex ratios of juvenile Bull Trout. Studies on adult Bull Trout often assume a 1:1 sex ratio (Rieman and Mclntyre 1993). However, with habitat fragmentation and increasing anthropogenic stressors, Bull Trout are facing variable selection based on life-history strategy. If one sex is more likely to adopt a particular life-history strategy, sex ratios may become biased, particularly in cases where one life-history strategy becomes an ecological sink (e.g., migratory fish out-migrating downstream over a barrier and not being able to return) (Schlaepfer et al. 2002). Additionally, in other salmonids, sex ratios have shown promise as a tool for identifying the approximate proportion of various life-history strategies present in a population (Ohms et al. 2013, 2018). We found that the sex ratio of age-1 Bull Trout was close to 1:1 in both tributaries, which is what is typically expected in taxa where sex determination is genetically controlled (Wedekind 2012). Although it is possible that sex could drive selective pressures prior to age 1, studies of other salmonids indicated that differences in traits based on sex may not be evident early in the life cycle (i.e., eggs and fry) (Régnier et al. 2015). We did observe deviations from a 1:1 sex ratio for Bull Trout older than age 1 and out-migrants in both streams; however, further research into the natural variability of sex ratios in Bull Trout is necessary. Understanding the natural variability expected will enable managers to discern between skewed sex ratios that are a result of natural variability, and skewed sex ratios that are a result of some underlying selective pressure. Human induced selection for or against certain life-history strategies could pose unnatural sex-dependent selection, which may have serious consequences for small populations (Wedekind 2012). Additionally, further research could enable the use of sex ratios as a tool for identifying the life-history strategies present in a population and the relative proportion of each life-history strategy (Ohms et al. 2013, 2018).

Our results indicated strong evidence that variation in water temperature metrics among reaches influenced the density of juvenile Bull Trout within tributaries, even at relatively small (<5 km) spatial scales. Despite the range in mean water temperatures between reaches being less than two degrees for both streams and years, and the range in maximum water temperatures being within three degrees, water temperature metrics were consistently able to explain variation in the density of Bull Trout. In both streams and years, the lowest elevation and warmest reaches contained the lowest densities of Bull Trout; however, the highest elevation and coldest reaches did not consistently contain the highest densities of Bull Trout.

The presence of curvilinear relationships between water temperature metrics and Bull Trout density indicates that within a certain water temperature range, Bull Trout may select for warmer temperatures. In laboratory studies of Bull Trout, and other salmonids, growth rate demonstrates a curvilinear relationship with water temperature, increasing to a peak after which the relationship becomes negative (Selong et al. 2001; Perry et al. 2015). Thus, the curvilinear relationship between water temperature and density of Bull Trout may reflect selection for water temperatures to maximize growth potential. Curvilinear relationships between density and water temperature have been observed in other salmonids within streams (Isaak and Hubert 2004).

Several factors likely contribute to the discrepancies between our results and results from past studies, which have generally found an entirely negative association between water temperature or elevation and juvenile Bull Trout (Paul and Post 2001; Dunham et al. 2003; Rieman et al. 2007). First, collecting water temperature data from reaches in close proximity revealed patterns that may have been missed if water temperature had only been measured at the lowest and uppermost reaches. Second, in East Fork Bull River, Bull Trout were absent from some of the lower reaches, and maximum water temperatures > 12 °C, indicating that the lowest reaches of East Fork Bull River may not be thermally suitable for Bull Trout. The relationships between water temperature or elevation and juvenile Bull Trout density in East Fork Bull River more closely resembled the negative relationships that would be expected based on large-scale studies (Paul and Post 2001; Dunham et al. 2003; Rieman et al. 2007). The presence of Bull Trout throughout Graves Creek, and maximum water temperatures < 12 °C, suggest that the entire sampling area in Graves Creek was within the thermal tolerance of Bull Trout. Curvilinear relationships were observed more consistently in Graves Creek than in East Fork Bull River. This phenomenon was described by Isaak and Hubert (2004), who hypothesized that the shape of relationships between water temperature and salmonid distribution are sensitive to the portion of the thermal range that is sampled. Under this hypothesis, negative linear relationships reflect water temperature gradients where the coldest reaches have reached or exceeded the maximum preferred water temperature (Isaak and Hubert 2004). Therefore, the negative linear relationships reflect the declining limb of a curvilinear relationship (Isaak and Hubert 2004).

We found that the highest density reaches in Graves Creek during both years, and in East Fork in 2020, were associated with the most stable water temperatures. Between both streams and seasons, reaches with the highest variation in water temperature had the lowest densities of Bull Trout. Stability of water temperature in streams may be affected by several factors, including canopy cover, precipitation, and groundwater inputs (Leach et al. 2016). Additional research is necessary to determine if groundwater inputs are the primary factor influencing water temperature stability in Graves Creek and East Fork Bull River. If groundwater is the primary factor influencing reach scale water temperature stability, the negative relationship between variation in water temperature and Bull Trout density may reflect a positive association between habitat selection and groundwater inputs. Groundwater has been shown to be an important factor in the distribution of salmonids within streams, with high groundwater influence associated with stable water temperatures, offering thermal refugia for temperature sensitive species (Power et al. 1999; Gamett 2002; Snyder et al. 2015; Larsen and Woelfle-Erskine 2018). Groundwater may also influence the distribution of juvenile Bull Trout through redd site selection by spawning females, particularly if dispersal of juvenile Bull Trout is low (Baxter and McPhail 1999). It is important that models predicting responses of Bull Trout to climate change consider the potential influence of groundwater inputs (Snyder et al. 2015). Depending on the strength of the relationship between groundwater and salmonids, groundwater inputs may lead to patchier distributions within tributaries under climate warming scenarios than would otherwise be expected (Snyder et al. 2015).

A notable limitation to this study was the date range when water temperature metrics were collected. The range was selected to enable the greatest number of reaches to be included, and because the primary objectives for this study were to assess the relationship between water temperature and density, rather than actual threshold values of water temperature. However, annual variation may have influenced whether the sampling period captured similar points in the annual water temperature fluctuations in each stream. Thus, inference about threshold values such as the maximum preferred water temperature is limited. Additional research that captures longer periods of water temperature data or is based on points in a water temperature profile rather than dates (i.e., a week before and a week after maximum summer temperature is reached) will allow for the identification of points within the thermal profile of Bull Trout that appear to influence distribution.

In this study, we focused on water temperature as past studies have identified water temperature to be one of the most important variables explaining the distribution of juvenile Bull Trout within streams (Dunham et al. 2003). Numerous other factors at the tributary scale may influence the distribution of juvenile Bull Trout at the tributary scale, such as substrate size, number of pools, and large-woody debris (Al-Chokhachy et al. 2010; Watson et al. 1997). Additionally, competition from non-native species and interspecific competition may influence selection of habitat within streams (Paul et al. 2000; Paul and Post 2001; Mcmahon et al. 2007), and these factors likely vary based on the tributary. Thus, while we did find evidence for the influence of water temperature on the density of Bull Trout, we acknowledge that other factors that we did not account for can influence their distribution. Additional research will allow for a more comprehensive understanding of the factors that influence the distribution of Bull Trout in Graves Creek and East Fork Bull River. In addition, research to quantify the habitat characteristics in reaches that appear to be highly selected for, such as reach 6 in Graves Creek, could inform restoration efforts to maximize preferred habitat.

Our results demonstrate how collecting water temperature data at fine-spatial scales can reveal relationships between the density of Bull Trout and water temperature that may be missed if data is collected at a larger scale (e.g., one temperature logger per stream, or temperature loggers placed at the highest and lowest reaches). Where a curvilinear relationship between density and water temperature was found, density declined rapidly following the peak in the relationship, even with small subsequent increases in temperature. If monitoring efforts are conducted at a scale that fails to capture variability in water temperature within the stream, it may be difficult to identify when and where this peak may occur, preventing proactive measures from being implemented

Our results have implications for the management and conservation of migratory Bull Trout at the tributary scale. Age-structure in both tributaries was similar to what we would expect from juvenile migratory Bull Trout based on other studies (Fraley and Shepard 1989; Zymonas 2006; Downs et al. 2006; Ratliff et al. 2015), indicating that age-structure can be a valuable tool to assess the life-history present in a population at the tributary level. Despite variation in age-structure between tributaries and within tributaries between years, the proportion of age-4 and older Bull Trout was consistently under 6%. Similar proportions of age-4 and older Bull Trout have been found in streams with predominantly migratory Bull Trout, and the proportion of age-4 and older Bull Trout is considerably higher in resident and mixed life-history strategy populations of Bull Trout (> 15%) (Zymonas 2006). Therefore, the identification of life-history strategies in Bull Trout populations may be possible by collecting scales and quantifying the proportion of age-4 and older Bull Trout. Collecting scales and quantifying age-structure requires a lower investment of time and resources when compared to efforts to confirm migration in populations using traps or PIT antennas. However, continued research of age structure in populations with known life-history strategies is necessary to identify the threshold value or range of threshold values that should be used, and to identify other factors that may influence the proportion of age-4 and older Bull Trout. The ability to identify the life-history strategies present in a population based on information collected at the tributary scale can enable biologist to determine if populations remain connected to larger habitats or if populations have become isolated. In some cases, such as a physical barrier, isolation may be easily observed; however, in other cases such as thermal barriers, isolation may be gradual and difficult to observe. Additionally, classifying life-history strategies in a population is necessary to determine if management efforts to restore migratory life-history strategies, such as translocations or trap-and-haul programs, are successful. We did not explicitly test for correlation between demographic characteristics and density; however, the demographic characteristics of juvenile Bull Trout in Graves Creek shared similarities with populations where an equilibrium state has been reached as a result of density-dependent processes (Paul et al. 2000; Johnston et al. 2007; Ratliff et al. 2015). Therefore, the variation in demographic characteristics of juvenile Bull Trout between Graves Creek and East Fork Bull River may be explained by the difference in densities and the availability of habitat between the tributaries. Identifying characteristics of a tributary and population that correlate with variation in demographic structure will enable more effective planning of active management efforts (e.g., number of spawning adult Bull Trout necessary to maximize recruitment in a tributary) and will allow for biologists to better anticipate how populations may respond to management actions.

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Tables

Table 1.1. Density of juvenile Bull Trout (number / m^2) and associated 95% prediction interval, elevation (m), mean water temperature (°C), mean maximum daily water temperature (°C), and coefficient of variation of mean water temperature from 15 August through 30 September by year and reach in Graves Creek and East Fork Bull River, Montana. Reaches where water temperature loggers were not recovered are not included.

Reach	Density (number/ m^2) (95% P.I.)	Elevation (m)	Mean temperature (°C)	Mean maximum daily temperature (°C)	CV of mean temperature
			Graves Creek (summer 2019)		
1	0.010 (0.010)	724.26	9.81	11.70	0.19
2	0.028 (0.011)	739.18	9.40	11.12	0.16
3	0.050 (0.011)	742.41	9.35	10.98	0.16
4	0.068 (0.008)	756.08	9.07	10.38	0.14
5	0.121 (0.012)	767.69	9.07	10.19	0.14
6	0.146 (0.012)	773.69	9.18	10.25	0.14
7	0.101(0.010)	779.65	9.07	10.08	0.14
9	0.100 (0.011)	807.51	9.03	9.80	0.17
10	0.089 (0.010)	816.68	8.86	9.58	0.17
11	0.081 (0.012)	836.53	8.76	9.45	0.17
12	0.062 (0.012)	851.01	8.63	9.32	0.17
			Graves Creek (summer 2020)		
1	0.026 (0.010)	724.26	9.34	11.05	0.16
2	0.026 (0.007)	739.18	9.09	10.74	0.15
3	0.031 (0.013)	742.41	9.04	10.61	0.14
4	0.039 (0.009)	756.08	8.83	10.12	0.13
5	0.066 (0.009)	767.69	8.85	9.94	0.13
6	0.105 (0.010)	773.69	8.92	9.99	0.13
7	0.063 (0.011)	779.65	8.82	9.84	0.13
9	0.085 (0.010)	807.51	8.79	9.70	0.14
10	0.041 (0.009)	816.68	8.64	9.52	0.14
11	0.065 (0.011)	836.53	8.56	9.44	0.14
12	0.051 (0.012)	851.01	8.44	9.35	0.14

Table 1.1 Continued

		East Fork Bull River (summer 2019)			
1	0.000 (0.000)	707.78	11.02	12.46	0.17
2	0.004 (0.004)	720.95	10.82	11.99	0.16
3	0.005 (0.003)	746.98	10.60	11.41	0.15
4	0.004 (0.004)	786.17	10.58	11.29	0.15
5	0.009 (0.003)	823.80	10.46	11.03	0.16
6	0.012 (0.003)	870.56	10.34	10.80	0.16
7	0.008 (0.003)	933.66	9.84	10.23	0.16
8	0.003 (0.004)	799.43	10.56	11.25	0.16
9	0.008 (0.003)	815.67	10.51	11.11	0.16
10	0.003 (0.004)	880.76	10.31	10.77	0.16
11	0.010 (0.003)	886.45	10.20	10.65	0.16
12	0.007 (0.004)	902.26	10.03	10.45	0.16
13	0.014 (0.003)	964.70	9.70	10.09	0.16
14	0.022 (0.005)	1012.87	9.41	9.84	0.17
15	0.020 (0.004)	1039.82	9.21	9.65	0.17
		East Fork Bull River (summer 2020)			
1	0.000 (0.000)	707.78	10.78	12.33	0.15
2	0.000 (0.000)	720.95	10.60	11.78	0.13
3	0.005 (0.003)	746.98	10.43	11.28	0.12
6	0.013 (0.004)	870.56	10.25	10.79	0.12
7	0.026 (0.004)	933.66	9.81	10.27	0.11
8	0.008 (0.004)	799.43	10.41	11.13	0.12
11	0.015 (0.003)	886.45	10.12	10.62	0.12
12	0.029 (0.006)	902.26	9.95	10.43	0.11
13	0.019 (0.005)	964.70	9.62	10.08	0.12
14	0.022 (0.005)	1012.87	9.36	9.87	0.12
15	0.017 (0.004)	1039.82	9.17	9.69	0.11

Table 1.2. Results from regression models of density of juvenile Bull Trout by reach in Graves Creek and the East Fork Bull River, Montana, and water temperature metrics, where D is the density of juvenile Bull Trout (number/m^2), E corresponds to the elevation of the reach (m), T_{mean} is the overall mean water temperature (°C), T_{max} is the mean maximum daily water temperature (°C), and CV is the coefficient of variation of water temperature. Parameter estimates, adjusted R^2, P-value, and residual degrees of freedom (d.f.), and Akaike weight by model. Models are ranked according to AIC$_c$ scores.

		Parameter Estimates (SE)			Adj.				Δ	
Model	Formula	ß$_0$	ß$_1$	ß$_2$	R^2	P-value	d.f.	AIC$_c$	AICc	Weight
		Graves Creek (summer 2019)								
1	$D \sim \beta_0 + \beta_1 E + \beta_2 E^2$	-13.80 (2.752)	0.0350 (0.007)	-2.20 x 10^{-5} (4.440 x 10^{-6})	0.74	<0.01	8	-43.19	0.00	0.81
2	$D \sim \beta_0 + \beta_1 T_{max} + \beta_2 {T_{max}}^2$	-4.322 (1.607)	0.876 (0.309)	-0.043 (0.015)	0.61	<0.01	8	-38.84	4.35	0.09
3	$D \sim \beta_0 + \beta_1 CV$	0.366 (0.099)	-1.818 (0.624)	-	0.43	0.05	9	-38.64	4.54	0.08
4	$D \sim \beta_0 + \beta_1 T_{mean} + \beta_2 {T_{mean}}^2$	-12.869 (6.103)	2.876 (1.327)	-0.159 (0.0720)	0.41	0.05	8	-34.44	8.75	0.01
		Graves Creek (summer 2020)								
1	$D \sim \beta_0 + \beta_1 CV$	0.263 (0.079)	-1.51 (0.567)	-	0.37	0.02	9	-47.56	0.00	0.79
2	$D \sim \beta_0 + \beta_1 E + \beta_2 E^2$	-6.532 (2.664)	0.017 (0.0067)	-1.032 x 10^{-5} (4.300 x 10^{-6})	0.39	0.06	8	-43.91	3.66	0.13
4	$D \sim \beta_0 + \beta_1 T_{max} + \beta_2 {T_{max}}^2$	-3.59 (2.60)	0.74 (0.51)	-0.04 (0.03)	0.31	0.09	8	-42.47	5.09	0.06
3	$D \sim \beta_0 + \beta_1 T_{mean} + \beta_2 {T_{mean}}^2$	-10.01 (7.71)	2.30 (1.74)	-0.13 (0.10)	0.11	0.26	8	-39.68	7.88	0.02
		East Fork Bull River (summer 2019)								

Table 1.2 Continued

1	$D \sim \beta_0 + \beta_1 T_{mean}$	0.120 (0.017)	-0.011 (0.002)	-	0.74	<0.0001	13	-123.48	0.00	0.71
2	$D \sim \beta_0 + \beta_1 E$	-0.037 (0.008)	0.00005 (<0.0001)	-	0.70	<0.0001	13	-121.11	2.37	0.22
3	$D \sim \beta_0 + \beta_1 T_{max}$	0.082 (0.014)	-0.007 (0.001)	-	0.65	<0.001	13	-118.74	4.74	0.06
4	$D \sim \beta_0 + \beta_1 CV$	-0.07 (0.04)	0.47 (0.26)	-	0.14	0.09	13	-105.41	18.07	0.00
			East Fork Bull River (summer 2020)							
1	$D \sim \beta_0 + \beta_1 T_{mean} + \beta_2 {T_{mean}}^2$	-1.993 (0.606)	0.406 (0.122)	-0.021 (0.006)	0.78	<0.0001	8	-75.88	0.00	0.37
2	$D \sim \beta_0 + \beta_1 T_{max}$	0.124 (0.024)	-0.010 (0.002)	-	0.67	0.001	9	-75.32	0.56	0.28
3	$D \sim \beta_0 + \beta_1 E + \beta_2 E^2$	-0.305 (0.102)	6.756 x 10^{-4} (2.392 x 10^{-4})	-3.491 x 10^{-7} (1.379 x 10^{-7})	0.77	0.001	8	-75.29	0.59	0.28
4	$D \sim \beta_0 + \beta_1 CV$	0.100 (0.022)	-0.706 (0.180)	-	0.59	<0.01	9	-72.79	3.09	0.08

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Figures

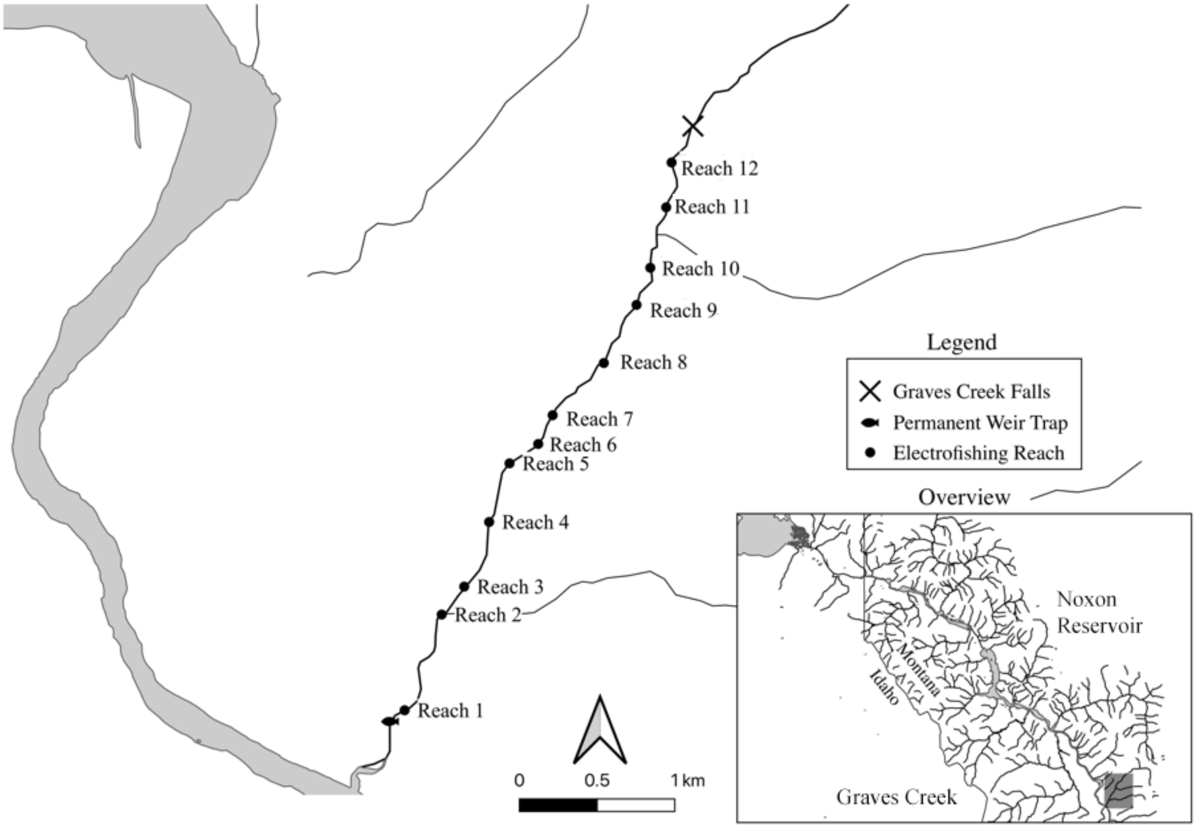

Figure 1.1. Study area on Graves Creek, Montana, with Graves Creek Falls, permanent weir trap, and electrofishing reaches delineated. Inset map depicts the location of Graves Creek in the Clark Fork watershed.

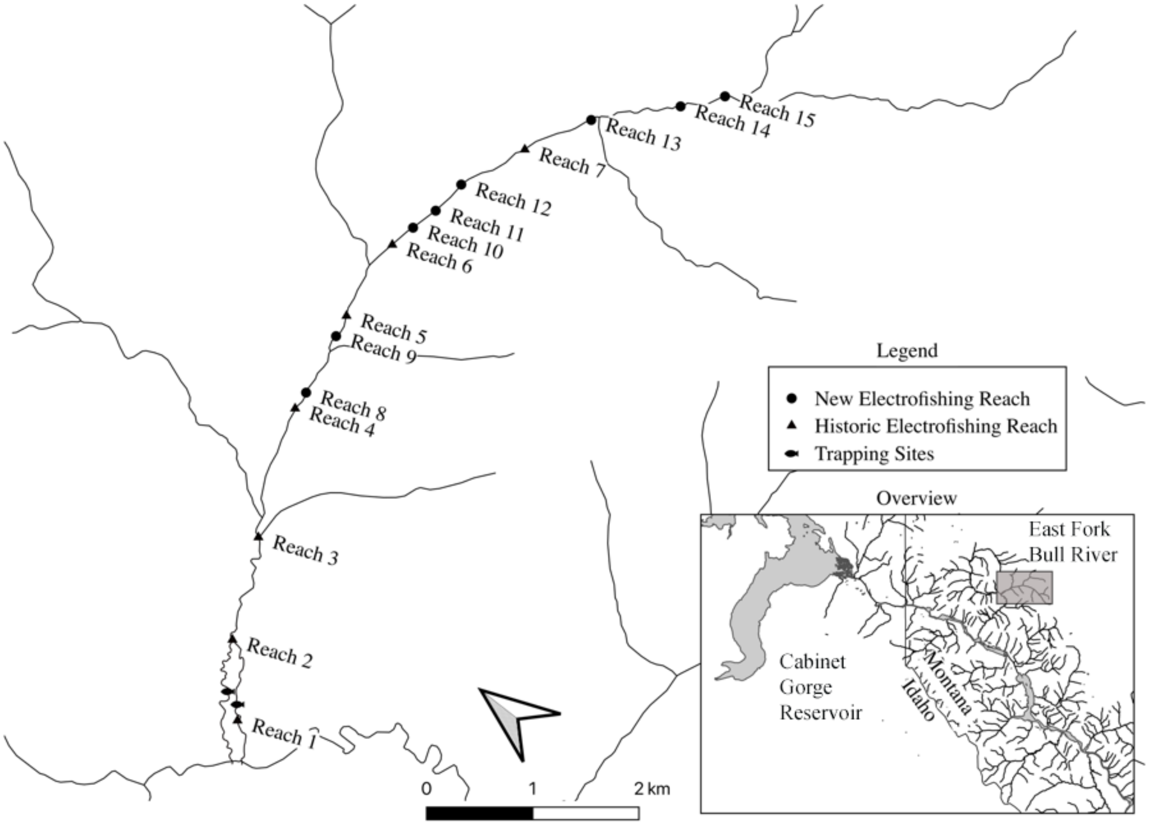

Figure 1.2. Study area on East Fork Bull River, Montana, with trapping sites, and electrofishing reaches delineated. Inset map depicts the location of East Fork Bull River in the Clark Fork watershed.

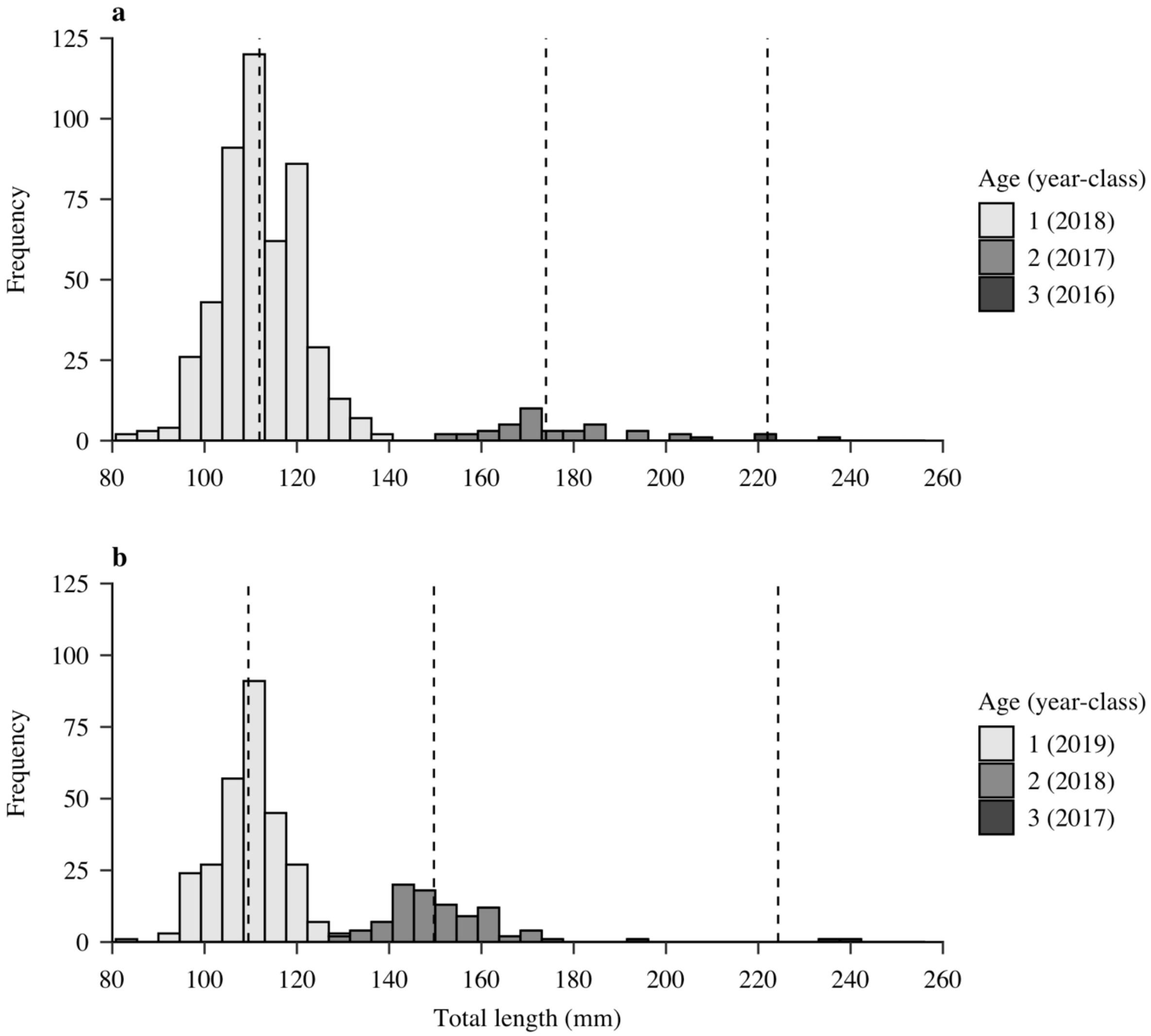

Figure 1.3. Length-frequency histogram of juvenile Bull Trout sampled in Graves Creek, Montana, in 2019 (n=530) (a) and 2020 (n=376) (b), with grey scale delineating age and the dotted lines delineating mean length by age.

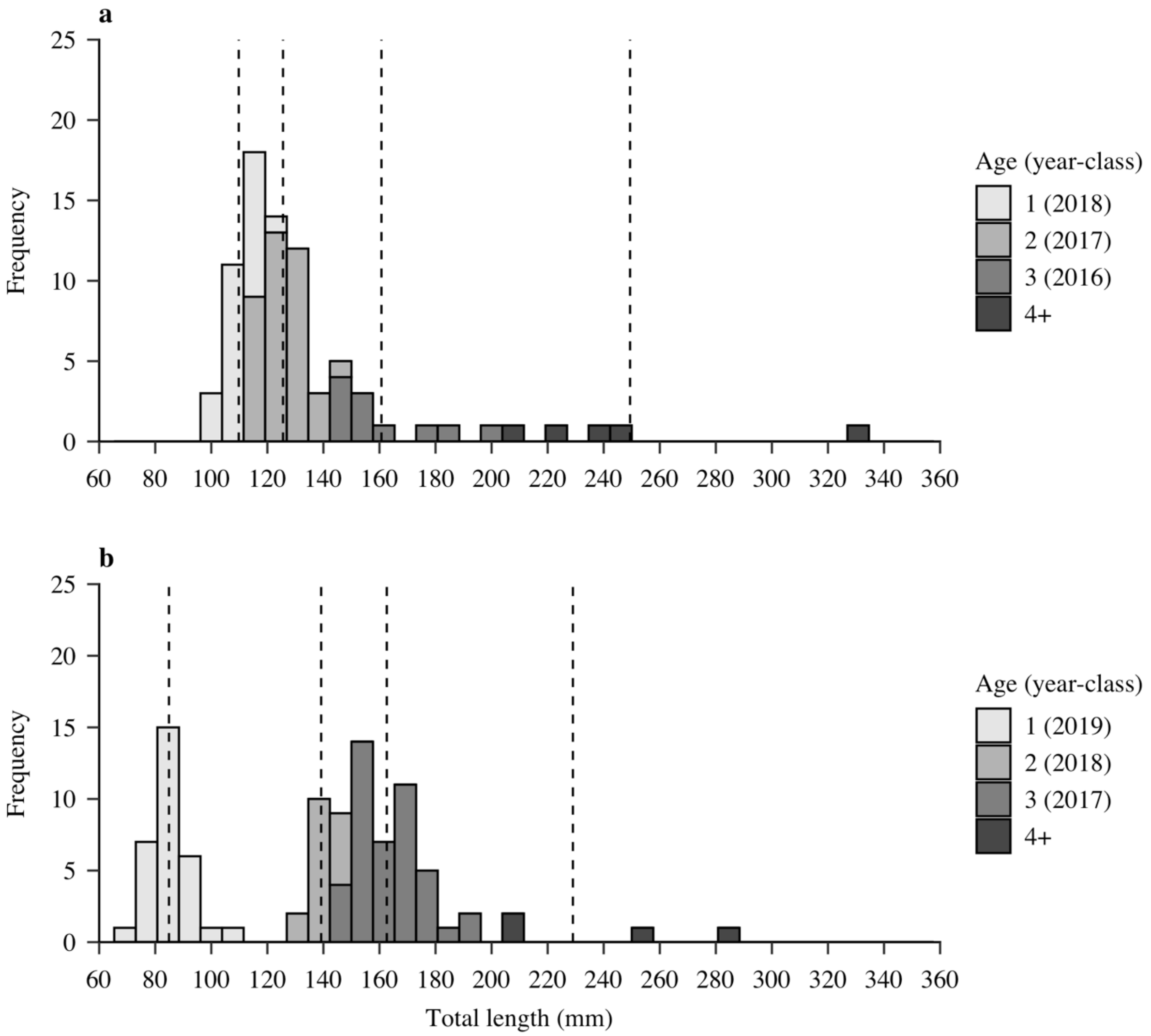

Figure 1.4. Length-frequency histogram of the sampled population of juvenile Bull Trout in East Fork Bull River, Montana, in 2019 (n=78) (a) and 2020 (n=96) (b), with grey scale delineating age and the dotted lines delineating mean length by age.

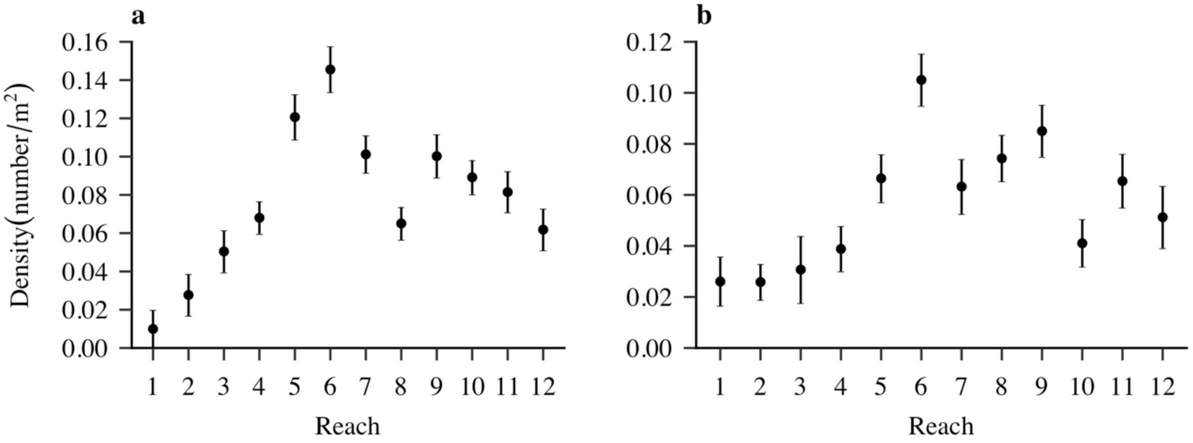

Figure 1.5. Density estimates for juvenile Bull Trout (number / m^2) by sampling reach in Graves Creek, Montana, during summer 2019 (a) and summer 2020 (b), vertical lines delineate the upper and lower 95% prediction intervals, and reaches ordered from downstream to upstream.

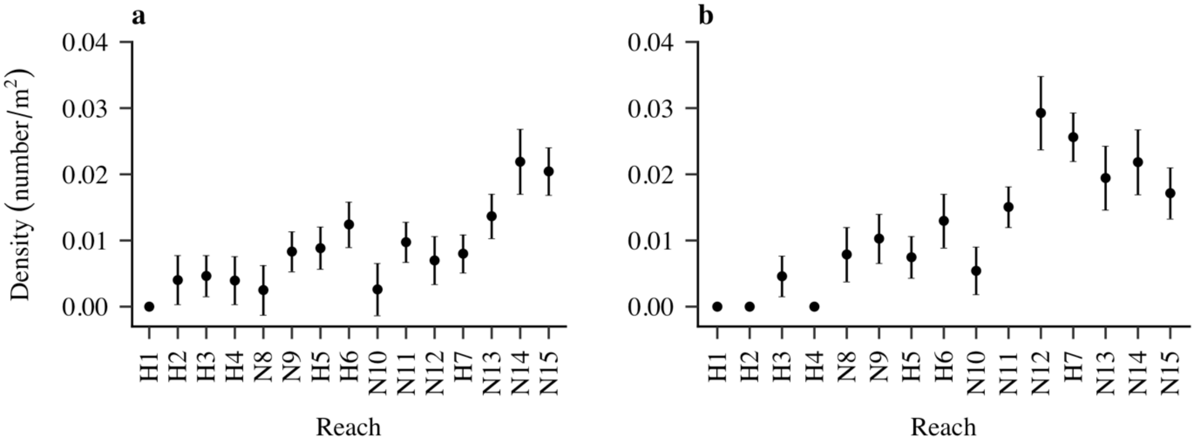

Figure 1.6. Density estimates for juvenile Bull Trout (number / m^2) by sampling reach in East Fork Bull River, Montana during summer 2019 (a) and summer 2020 (b), vertical lines delineate the upper and lower 95% prediction intervals. Reaches are ordered from downstream to upstream, with ‘H’ representing a historic sampling reach, and ‘N’ representing a new sampling reach.

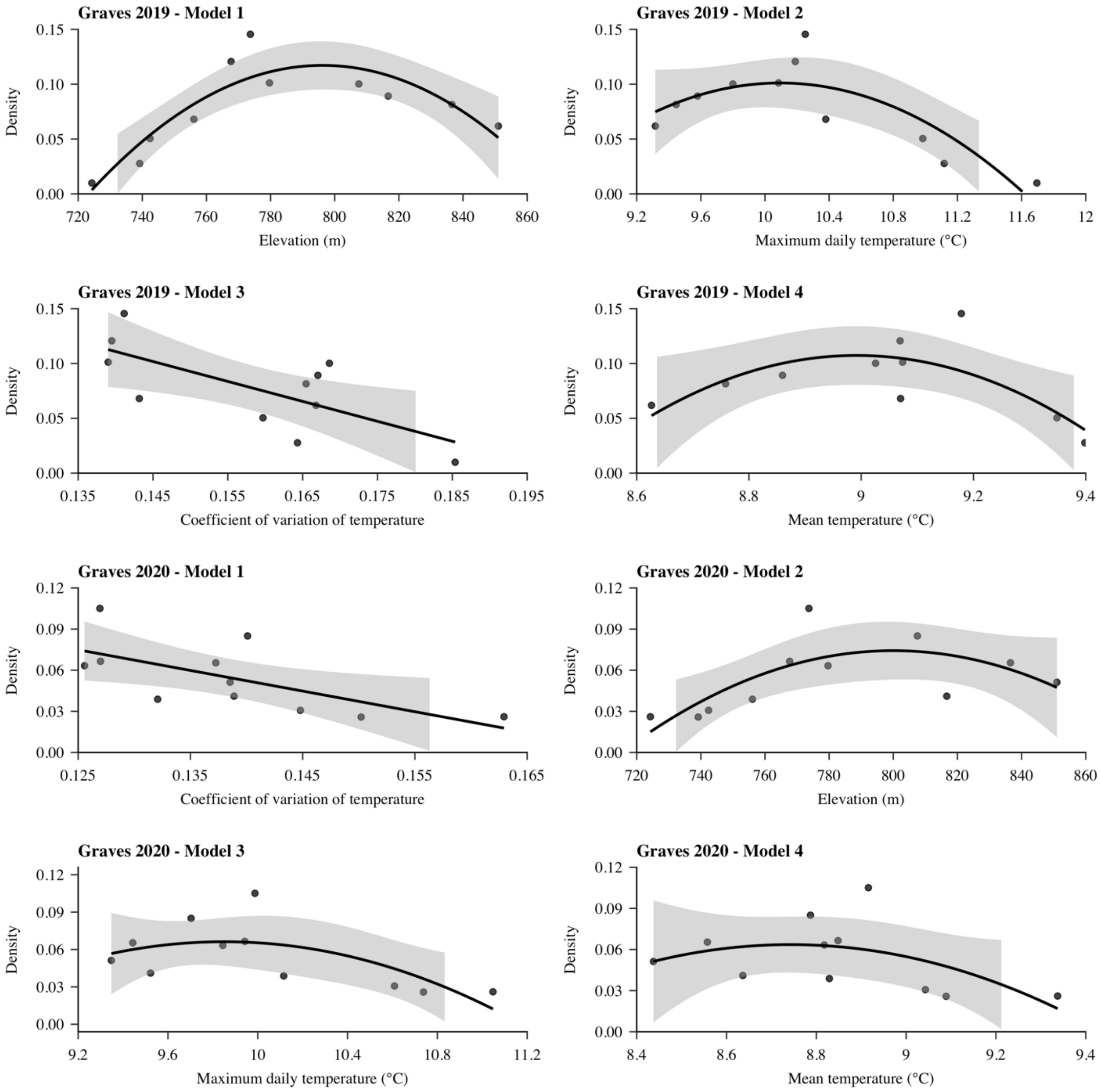

Figure 1.7. Relations between the density (number/m^2) of juvenile Bull Trout and environmental variables in Graves Creek, Montana (Graves), symbols represent observed values, lines delineate fitted regression line, and the shaded areas delineate 95% confidence intervals. Model number relates to models from Table 1.2.

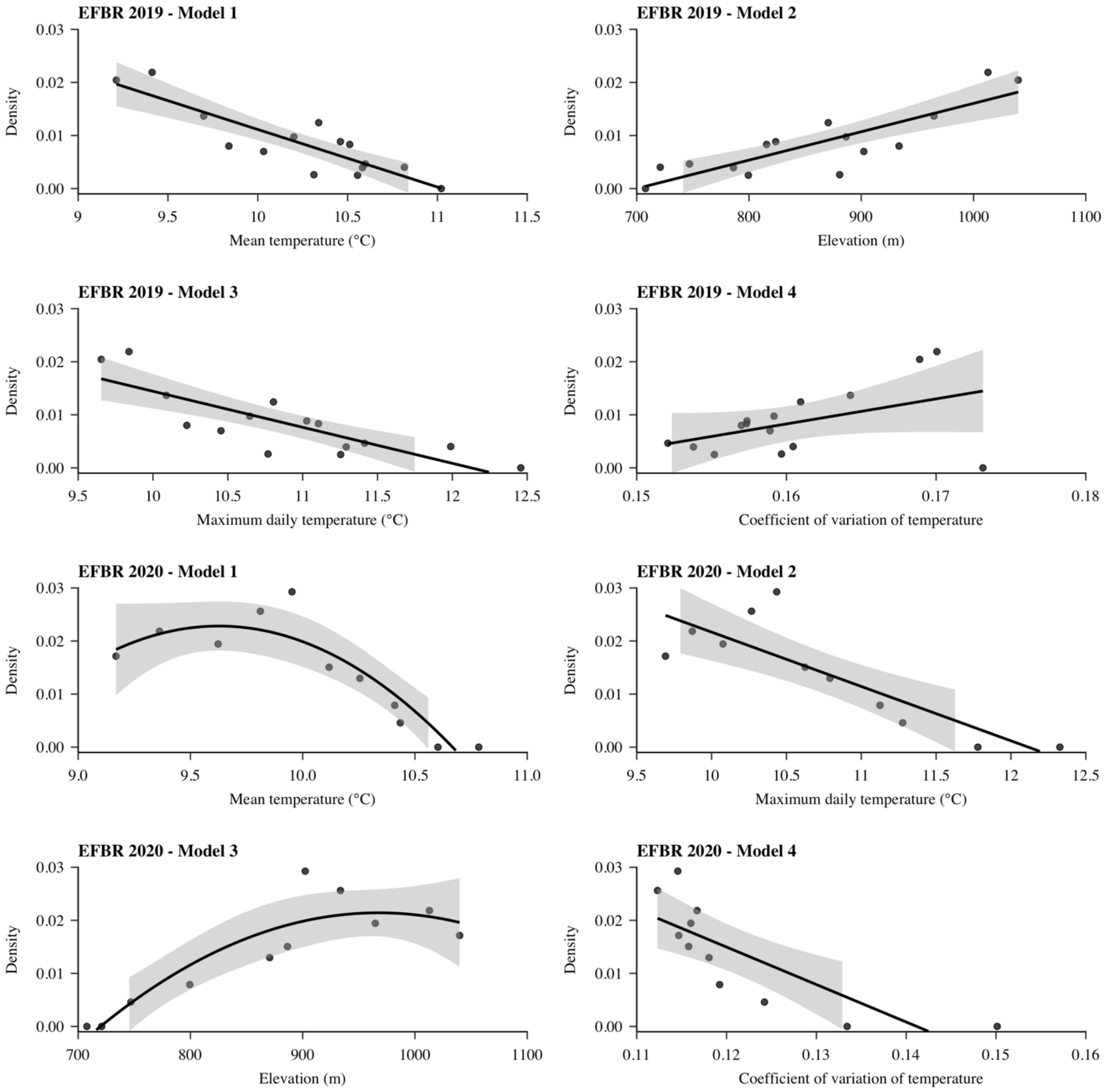

Figure 1.8. Relations between the density (number/m^2) of juvenile Bull Trout and environmental variables in East Fork Bull River, Montana (EFBR) symbols represent observed values, lines delineate fitted regression line, and the shaded areas delineate 95% confidence intervals. Model number relates to models from Table 1.2.

CHAPTER TWO

SEASONAL CAPTURE EFFICIENCIES INFLUENCES KNOWLEDGE OF UNDERLYING OUT-MIGRATION DYNAMICS IN BULL TROUT POPULATIONS WITH JUVENILE DOWNSTREAM TRAP-AND-HAUL PROGRAMS

Contribution of Authors and Co-Authors

Manuscripts in Chapter 1, 2, and 3

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Co-Author: Christopher S. Guy

Contributions: Obtained funding, conceived study, assisted with implementation, discussed analyses and results, edited manuscript.

Co-Author: Eric W. Oldenburg

Contributions: Obtained funding, conceived study, assisted with implementation, discussed analyses and results, edited manuscript.

Co-Author: Thomas E. McMahon

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Manuscript Information

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North American Journal of Fisheries Management

Status of Manuscript:

__x__ Prepared for submission to a peer-reviewed journal

____ Officially submitted to a peer-reviewed journal

____ Accepted by a peer-reviewed journal

____ Published in a peer-reviewed journal

Abstract

Trap-and-haul programs can maintain connection among habitats for migratory salmonids in fragmented systems. To conserve diversity within and among life-history strategies, downstream trapping and transport of juvenile salmonids should ideally mimic the natural, underlying out-migration dynamics of the population. A two-way trap-and-haul program is implemented in the lower Clark Fork River, Montana, to conserve adfluvial Bull Trout *Salvelinus confluentus*. We used PIT technology to assess whether downstream capture efforts are effectively capturing variation in the out-migration dynamics of juvenile Bull Trout in Graves Creek and East Fork Bull River, two primary tributaries in the program. We tagged 821 juvenile Bull Trout in Graves Creek and 144 Bull Trout in East Fork Bull River and used these tagged Bull Trout in conjunction with stationary PIT antennas to monitor out-migration and evaluate efficiency of the downstream trapping program. Capture efficiency in Graves Creek varied substantially from autumn to spring, with 89 – 96% of autumn out-migrating Bull Trout captured, and 10% of spring out-migrating Bull Trout captured. Monitoring tagged Bull Trout revealed that the low spring capture efficiency likely biased previous knowledge of the timing and magnitude of annual out-migration events in Graves Creek. Overall, we found that Bull Trout transported during the autumn out-migration periods generally reflect the natural out-migration dynamics of the population; however, Bull Trout that out-migrate in the spring are currently underrepresented in the downstream transport program. In the East Fork Bull River, were not able to quantify capture efficiency or estimate underlying out-migration dynamics due to low sample size of tagged out-migrating Bull Trout. By understanding the underlying out-migration dynamics of the Bull Trout population in Graves Creek, management of the

downstream trapping efforts can focus on minimizing potential selection for or against out-migrants based on timing and age at out-migration. Minimizing selection will conserve variation within the adfluvial life-history strategy, and therefore maximize resilience of the adfluvial Bull Trout populations.

Introduction

As anthropogenic threats to the biodiversity of freshwater fish species increase, there is an increasing need to focus conservation efforts on actions that will increase the resilience of populations (Waldman et al. 2016); where resilience is defined as the ability of a population to persist in the face of disturbance or change (Holling 1973). Many species of salmonids express diverse life-history strategies, thought to be an evolutionary adaption that allows species to persist in variable environments (Schindler et al. 2010; Tamario et al. 2019). Bull trout *Salvelinus confluentus*, a species of char listed as threatened under the United States Endangered Species Act, exhibit variation in discrete life-history strategies (i.e., resident, migratory), and variation in traits within discrete life-history strategies (i.e., age or timing of migration) (Rieman and Mclntyre 1993; Al-Chokhachy and Budy 2008; Howell et al. 2016) that occurs among and within populations (Rieman and Mclntyre 1993; Al-Chokhachy and Budy 2008; Howell et al. 2016). Migratory individuals offer many benefits to local Bull Trout populations, such as increased fecundity associated with large body size, and the ability to facilitate gene flow among local populations (Rieman and Allendorf 2001; USFWS 2015a). Additionally, by diversifying the spatial-temporal habitat use of a population, migratory individuals decrease the probability of a local extirpation without opportunity for recolonization (Burton 2005).

Widespread habitat fragmentation due to physical and thermal barriers, and other habitat degradation have caused declines, and in some Bull Trout populations a complete loss of the migratory life-history strategy (Rieman et al. 1997; Rieman and Allendorf 2001). Restoring and maintaining diversity in life-history strategies of Bull Trout populations is vital to ensure that the species is resilient to future changes and is considered a primary goal of the USFWS Bull Trout recovery plan (USFWS 2015a). In some cases, the migratory life-history component of Bull Trout populations may be restored by the removal of a barrier such as a dam, allowing habitats to reconnect (Quinn et al. 2017; Brenkman et al. 2019). However, barrier removal is often not an option; therefore, there is an increasing need for solutions to restore and maintain migratory life-history strategies in systems that remain fragmented by barriers. One solution is the implementation of a trap-and-haul program, where fish are physically moved upstream or downstream of a barrier. Trap-and-haul programs have been employed for a variety of species, including anadromous salmonids (Kock et al. 2018; Naughton et al. 2018), lamprey (Corbett et al. 2014), and small-bodied fish species (Harris et al. 2019).

In the early 2000s, a two-way trap-and-haul program was implemented to re-establish connectivity between local Bull Trout populations in the lower Clark Fork River and Lake Pend Oreille, restoring the historic adfluvial migratory life-history component of the lower Clark Fork River population (Neraas and Spruell 2001; Epifanio et al. 2003; Dehaan et al. 2011). In this program, adult Bull Trout are captured at the base of Cabinet Gorge Dam and transported upstream to their most likely region of origin, determined by PIT tag for previously tagged fish or real-time genotyping for untagged fish, to allow access to their natal streams to spawn (Dehaan et al. 2011). The juvenile Bull Trout trap-and-haul program (hereafter, downstream program) was implemented to address concerns that passage through the reservoirs caused a high amount of mortality on out-migrating juveniles due to seasonally warm water temperatures and the presence of non-native piscivorous species (USFWS 2015b). In the downstream program, juvenile Bull Trout are captured within their natal streams as they begin to out-migrate and are transported directly to Lake Pend Oreille. Juvenile Bull Trout that are not captured by the traps enter the reservoir system and either migrate volitionally downstream to Lake Pend Oreille or use the reservoir system as a surrogate for the lake habitat (hereafter, “reservoir-type”).

Trap-and-haul programs can enable connectivity in populations when physical characteristics of the dam and associated habitat, or characteristics of the species, render passive efforts such as fish ladders ineffective (Bunt et al. 2012; Silva et al. 2018; Harris et al. 2019). However, trap-and-haul programs are resource intensive and the high degree of human intervention that is involved may have unintended consequences. The extent of these consequences, such as altering behavior, influencing migration timing, and unintentionally imposing selective pressure may be difficult to fully understand and quantify (Budy et al. 2002; Muir et al. 2006; Al-Chokhachy et al. 2015). Multiple aspects of trap-and-haul programs may impose selective pressures, such as size selectivity of the gear used to capture fish for transport, or selection on timing of out-migration because of the timing and duration of trapping seasons. To effectively manage trap-and-haul programs for maximum benefit to the population, it is fundamental to understand the underlying out-migration dynamics of the population, and how capture methods may influence these dynamics. Without this understanding, natural resource agencies may inadvertently reduce the life-history variation present in populations by imposing selective pressures, ultimately reducing the resilience of the population, rather than increasing resilience (Schindler et al. 2010; Kock et al. 2020).

The two-way trap-and-haul program has been successful in restoring the adfluvial life-history strategy of Bull Trout that use Lake Pend Oreille for growth to maturity (i.e., successful returns of juvenile transports) (DeHaan and Bernall 2013). However, the number of Bull Trout captured in the traps has served as the primary source of information driving management decisions. Using the number of Bull Trout captured in the traps as a metric of success without explicitly quantifying and accounting for capture efficiency has led to a limited and biased knowledge base regarding the underlying out-migration dynamics of these populations. Therefore, it is unknown whether the downstream trapping program is effectively capturing variation in the age-at-out-migration and timing of out-migration, or whether the trapping program is imposing selection for certain traits. To address this knowledge gap, substantial investments into infrastructure have been made to facilitate applied research in Graves Creek and East Fork Bull River, two of the primary streams in the downstream program. The infrastructure includes multiple stationary, permanent PIT antennas located in or around the trapping sites on each stream, which operate year round. Stationary PIT antennas have been widely used to better understand multiple aspects of fish behavior in streams, such as movement and out-migration (Horton et al. 2007), and habitat use (Greenberg and Giller 2000).

We used the stationary PIT antennas to develop a better understanding of the underlying out-migration dynamics of juvenile adfluvial Bull Trout in Graves Creek and East Fork Bull River, and to assess how the current downstream trapping program may be influencing these dynamics. We sought to answer the following questions: 1) what is the current capture efficiency of the downstream traps; 2) what is the total number of out-migrating Bull Trout from each tributary by age, adjusted for capture efficiency of the traps; 3) what is the distribution of out-migration events annually; and 4) do the downstream trapping methods effectively capture variation in size, age, and timing of out-migrating Bull Trout? Understanding the underlying out-migration dynamics of the populations will enable the identification of potential sources of selection within the downstream trapping program. Identifying potential sources of selection will inform management to ensure the downstream program continues to conserve the adfluvial life-history strategy, while also conserving variation within the adfluvial life-history strategy of Bull Trout, thus increasing the resiliency of the populations.

Study Site

The Clark Fork River originates near Butte, Montana, and flows in a north-west direction for nearly 500 km before reaching Lake Pend Oreille, Idaho. Historically, the lower Clark Fork River served as a migration corridor for adfluvial Bull Trout, which would spawn and rear in Montana tributaries, before migrating downstream to Lake Pend Oreille for growth to maturity (Pratt 1985). From 1913 to 1959, three hydropower dams were constructed on the lower Clark Fork River with no fish passage facilities (Figure 2.1). The dams isolated at least 15 local Bull Trout populations (i.e., a population of Bull Trout that spawn within the same tributary) that were previously migratory (Pratt and Huston 1993; USFWS 2015a). The downstream most dam, Cabinet Gorge Dam, is located in Idaho approximately 16 km upstream from confluence of the Clark Fork River with Lake Pend Oreille (Figure 2.1). Cabinet Gorge Reservoir spans approximately 32 km upstream, to Noxon Rapids Dam (Figure 2. 1). Noxon Reservoir spans for 60 km upstream from Noxon Rapids Dam to Thompson Falls Dam (Figure 2.1).

Graves Creek enters the north side of Noxon Reservoir (Figure 2.1) as a fourth order stream with a length of approximately 21 km. Graves Creek Falls is a natural barrier to upstream fish passage located at river kilometer 5.2, and Bull Trout distribution is limited to the reach below the falls, where this study occurred. Despite the small area of habitat inhabited by Bull Trout, Graves Creek has consistently contributed a large proportion of transports to the downstream program (DeHaan and Bernall 2013). Bull Trout and Westslope Cutthroat Trout

Oncorhynchus clarkii lewisi, are the most predominant species present below Graves Creek Falls. From 2002 through 2012, juvenile Bull Trout in Graves Creek were captured for the trap-and-haul program using screw traps and temporary weir traps. In 2012, a permanent, concrete bedded weir trap was constructed in Graves Creek, and operation of the permanent weir began in 2013. A permanent PIT-monitoring station is also present, with two antennas located upstream of the weir, two integrated into the weir, and two antennas downstream of the weir (Figure 2.2).

East Fork Bull River is approximately 13-km long and enters the Bull River as a fourth order stream (Figure 2.1). Near the confluence with the Bull River, East Fork Bull River splits into a north channel and a south channel, which remain separated at the confluence with the Bull River (Figure 2.1). The species assemblage in East Fork Bull River varies longitudinally. The upper reaches are primarily inhabited by Bull Trout and Westslope Cutthroat Trout. The lower reaches of East Fork Bull River have a higher density of non-native species, including Rainbow Trout *Oncorhynchus mykiss*, Brown Trout *Salmo trutta*, and Brook Trout *Salvelinus fontinalis*. Two temporary weirs and two screw traps are operated in the lower East Fork Bull River to capture out-migrating juvenile Bull Trout for the downstream program (Figure 2.1). Temporary weirs are operated in both the north channel and south channel when conditions allow. Two screw traps are operated in the south channel when discharge and debris cause the weirs to be non-functional (generally early April through late June). Two full span PIT antennas are located downstream of the trapping sites in each channel.

Methods

Field sampling methods

During the summer of 2019 and the summer of 2020, juvenile Bull Trout were sampled at 12 100-m reaches in Graves Creek, and 15 100-m reaches in the East Fork Bull River (Figure 2.1). A backpack electrofisher (Smith-Root, LR-24 model) was used in a downstream direction to a block net. All fish that were sampled were measured for total length (mm), weight (g), and scanned for the presence of a PIT-tag. If a PIT-tag was not detected, Bull Trout > 100 mm received a 12-mm full duplex PIT tag. Prior to tag insertion, Bull Trout were anesthetized with Aqui-S. A disinfected needle or Biomark MK25 injector was used to insert the PIT tag into the anterior dorsal sinus of the Bull Trout. Bull trout were returned to live cars and once recovered, were released throughout the sampling reach. We did not attempt to capture or enumerate age-0 Bull Trout because they were not fully recruited to the gear, and would not meet the minimum size requirement for PIT-tagging. We tagged 821 juvenile Bull Trout in Graves Creek and 144 Bull Trout in East Fork Bull River.

Trapping operations

In Graves Creek, out-migrating Bull Trout were captured using the permanent, concrete bedded weir trap located at river kilometer 0.5 (Figure 2.1). The permanent weir trap was comprised of two rows of weir panels attached to a concrete slab. The upstream row was comprised of nine panels with 13-mm diameter vertical pickets on each panel, and 13-mm space between panels. The downstream row was comprised of seven panels with 13-mm diameter vertical pickets on each panel, and 19-mm space between panels of vertical pickets. The upstream row guided downstream-moving fish to a recessed channel in the concrete that terminated at the entrance to a 254-mm pipe. Fish traveled down the pipe that terminated with a short (~254 mm) outfall into a trap box. The downstream weir guided upstream-moving fish to the same recessed channel that terminated at the entrance to a trap box. The permanent weir trap was operated in the autumn of 2019 (4 September 2019 – 27 November 2019), spring of 2020 (15 April 2020 – 2 July 2020), and the autumn of 2020 (2 September 2020 – 20 November 2020). The weir trap was checked daily for fish and cleared of debris. During the autumn trapping seasons, panels were lowered on the trap once per week from the start of trapping through 6 October to allow for volitional passage of adult Bull Trout, which left the trap partially fishing. During the spring trapping season, all panels were lowered and the trap box was removed each weekend due to logistic limitations. In East Fork Bull River, out-migrating Bull Trout were captured during the same durations as stated above, using a combination of two rotary screw traps in the south channel when flows were high and a temporary weir trap in the north and south channel when conditions allowed (Figure 2.1).

All fish captured in the traps were measured for total length (mm), weight (g), and scanned for the presence of a PIT-tag. Bull Trout that met the minimum size limit for transport (>= 120 mm) were transported to a release site below Cabinet Gorge Dam. Bull Trout that were under the size limit were released below the traps. Bull Trout < 100 mm captured in the trap were not included in the results because they did not meet the minimum size requirement for tagging.

Age and length of out-migrating Bull Trout

Scales were removed from juvenile Bull Trout to estimate age structure during summer sampling. Scales were removed from all sampled Bull Trout above the lateral line ventral to the leading edge of the dorsal fins using a clean knife. In the lab, scales from ten fish were randomly selected from each 10-mm length class for aging. Photographs of the scales were acquired using a Leica microscope, and the photographs of scales were aged individually by two readers. Readers did not have knowledge of fish length prior to aging. When age estimates did not agree between readers, scales were aged again, and on rare occasions a third independent reader was consulted to determine the age. If an agreement could not be reached or the quality was deemed too low to accurately determine an age, the sample was excluded, and an alternate fish was randomly selected from the size class. In East Fork Bull River, Bull Trout that were estimated to exceed 4 years were pooled because accuracy of ageing from scales declines at older ages (Zymonas and McMahon 2009). The 'FSA' package in R (Ogle et al. 2020) was used to construct a length-at-age key. The length-at-age key was then used to assign ages to all Bull Trout sampled, following methods outlined by Isermann and Knight (2005). Year-class was also assigned based on the year that the Bull Trout emerged (e.g., the 2018-year-class was a product of redds in 2017) to enable tracking of cohorts through time. Age structure of out-migrating Bull Trout during the trapping seasons was estimated using Bull Trout that were previously tagged and aged during summer sampling, and subsequently captured in the trap. A new length-at-age was constructed based on the length of the Bull Trout when captured in the trap and used to assign ages to all Bull Trout captured in the trap. A Welch's *t*-test was conducted in R (R Core Team 2020) to test for interannual variation in mean length of Bull Trout captured in the trap by age.

Capture efficiency

In Graves Creek, we assessed capture efficiency of the permanent weir trap and overall capture efficiency of the downstream trapping program using the stationary PIT antennas and out-migrating Bull Trout that were tagged in summer sampling (i.e., fish tagged in 2019, 2020).

During trapping seasons, if a Bull Trout approached the trap and was detected on at least one upstream antenna (A6, A5) and was subsequently captured in the trap, it was considered a capture (Figure 2.2). If a Bull Trout was detected on at least one downstream antenna (A1, A2), without being captured in the trap, it was considered a missed fish (Figure 2.2). Missed fish were further grouped into the following categories, fish missed when the trap was partially fishing for volitional passage, fish missed when the trap was not in place for weekends or holidays, fish missed when the trap was in place but partially fishing (e.g., clogged with debris, overtopped), and fish missed for unknown reasons (i.e., trap appeared to be fully fishing).

Capture efficiency of the weir was calculated as the proportion of captured fish that were previously tagged out of the total number of tagged Bull Trout that out-migrated (i.e., captured fish and missed fish). Capture efficiency was calculated by age-class for each season (autumn 2019, spring 2020, autumn 2020). Calculations for capture efficiency of the weir did not include fish missed during volitional passage days, or fish missed when the trap was not fishing for weekends or holidays. Overall capture efficiency was calculated including fish missed for any reason, including volitional passage and fish missed when the trap was not fishing for weekends or holidays. For East Fork Bull River, capture efficiency of each trap (i.e., north channel, south channel) was calculated using the methods described above, with fish that were detected on at least one antenna during the trapping season being considered missed.

Total number of out-migrants

Total number of out-migrants by age-class during each trapping season in Graves Creek and East Fork Bull River was estimated using a Peterson equation with a Chapman modification, which was modified to enable estimation with the PIT-antennas (Volkhardt et al. 2007):

$$\widehat{N}_i = \frac{(M_i+1)(n_i+1)}{(m_i+1)} - 1,$$

where, during discrete time period i, M_i is the total number of tagged Bull Trout that out-migrated and were either captured in the trap or missed by the trap, n_i is the total number of Bull Trout captured in the trap (including tagged and untagged Bull Trout), and m_i is the total number of tagged Bull Trout that out-migrated and were captured in the trap. Total number of out-migrants was calculated separately for each age-class, with the duration of the trapping season representing the discrete time period i. The calculation for the total number of out-migrating Bull Trout included all fish that were missed for the season, including fish missed on volitional passage days and on weekends and holidays. Variance was calculated using the following equation developed by Seber (1970):

$$V(\widehat{N}_i) = \frac{(M_i+1)(n_i+1)(M_i-m_i)(n_i-m_i)}{(m_i+1)^2(m_i+2)}.$$

During the autumn 2020 trapping season on Graves Creek, an American Mink *Neovison vison* entered the trap box and removed multiple fish. Mink predation was first suspected when multiple tagged fish were detected on A3 as they entered the trap box, but subsequently disappeared (Figure 2.2). The presence of an American mink preying on fish in the trap box was confirmed with a game camera. Of the 85 tagged age-2 Bull Trout that entered the trap box, 33% are believed to have been removed by American mink. The percentage of tagged fish that were removed by American mink was applied to the number of untagged age-2 Bull Trout captured to estimate the total number of Bull Trout that may have been removed by American mink.

Timing of out-migration and overall efficiency of downstream trapping methods

Out-migration from Graves Creek was monitored using the stationary PIT antennas. The upstream (A6, A5) and downstream (A1, A2) antennas were operated year-round, while A3 and A4 were only operational during the trapping seasons (Figure 2.2). Bull trout were considered out-migrants if they were detected on at least one downstream antenna or captured in the trap. Overall efficiency of the current downstream trapping efforts was assessed using the fates assigned above for the trapping seasons, along with fish that out-migrated during seasons when the trap was not fishing. In East Fork Bull River, the four total antennas were operated year-round, and Bull Trout were considered out-migrants if they were detected on any antenna in the East Fork Bull River. In Graves Creek and East Fork Bull River, out-migration of tagged Bull Trout was tracked over the duration of the study (July 2019 – December 2020), with data downloaded periodically. Out-migration date was assigned to a fish on the last date the fish was detected.

Results

Capture efficiency of traps

Capture efficiency of the permanent weir varied substantially between autumn and spring trapping seasons (Table 2.1). During the autumn 2019 trapping season, capture efficiency of the permanent weir in Graves Creek varied by age class, with the lowest efficiency for age-1 Bull Trout (Table 2.1). Capture efficiency for age-2 Bull Trout was 95% (Table 2.1), and capture efficiency was 100% for age-3 Bull Trout (Table 2.1). Mean capture efficiency of the weir for all age-classes was 93%, and overall efficiency was 89% because of three fish out-migrating on volitional passage days (Table 2.1). In the spring 2020 trapping season, capture efficiency estimation was limited to age-2 Bull Trout (age-1 Bull Trout were below the minimum tagging length during summer sampling). Capture efficiency during the spring was substantially lower than the autumn, at 14% for age-2 Bull Trout (Table 2.1). The majority of Bull Trout in the spring were missed when the weir was partially fishing (Table 2.1). Overall efficiency during the spring was 10%, a result of 20 fish out-migrating during weekends when the trap was not operating (Table 2.1). Capture efficiency during the autumn 2020 trapping season was high overall, with 100% estimated efficiency for age-1 and age-3 Bull Trout, and 97% efficiency for age-2 Bull Trout (Table 2.1). Mean capture efficiency of the weir for all age-classes was 99%, and overall efficiency was 96% because of four fish out-migrating on volitional passage days and three fish out-migrating on holidays (Table 2.1).

In East Fork Bull River, low sample sizes of tagged, out-migrating Bull Trout limited the inferences that could be made regarding capture efficiency and total number of out-migrating Bull Trout. In the autumn of 2019, 31 Bull Trout were captured in the trap, and two previously tagged Bull Trout were missed by the trap. During the spring of 2020, two Bull Trout were captured in the trap, and one tagged fish was detected and missed by the trap. Due to the lack of tagged, trapped out-migrants, we could not estimate capture efficiency or the total number of out-migrants. During the autumn 2020 trapping season, 45 untagged Bull Trout were captured in the traps, one tagged Bull Trout was captured, and 13 tagged Bull Trout were missed. These data indicate a capture efficiency of 7.6%; however, the use of two traps in two channels and the small sample size adds uncertainty to the estimate.

Total number of out-migrants and age structure

The estimated number of Bull Trout out-migrants from Graves Creek was highest in the autumn of 2019 (Table 2.1). In autumn 2019, a total of 704 Bull Trout were captured, and an estimated 840 (96) (mean [95% C.I.]) Bull Trout out-migrated (Table 2.1). The age-structure of Bull Trout captured in the trap was 71% age 1, 29% age 2, and less than 1% age 3 (Table 2.1). The estimated age structure of the total number of Bull Trout out-migrating was similar, and was 72% age 1, 28% age 2, and less than 1% age 3 (Table 2.1). During the spring 2020 trapping season, 50 age-2 Bull Trout were captured in the trap, and the total estimated number of age-2 out-migrating Bull Trout was 443 (221) (Table 2.1). Two age-1 Bull Trout were captured in the trap; however, we were not able to estimate the total number of age-1 out-migrants because age-1 Bull Trout were too small to tag prior to spring out-migration (Table 2.1). In autumn 2020, 616 Bull Trout were captured in the trap, and the total estimated number of out-migrating Bull Trout was 678 (37) (Table 2.1). The age-structure of Bull Trout captured in the trap was 12% age 1, 87% age 2, and 1% age 3 (Table 2.1). The estimated age structure of the total number of Bull Trout out-migrating from Graves Creek was similar, and was 11% age 1, 88% age 2, and 1% age 3 (Table 2.1).

In Graves Creek, mean length of age-1 Bull Trout captured in the trap during the autumn trapping season was similar between 2019 and 2020 ($t = -0.5$, df = 135.10 $P = 0.6$) (Figure 2.3). Mean length of age-2 Bull Trout captured during the autumn 2019 trapping season was larger than the mean length of age-2 Bull Trout captured during the 2020 autumn trapping season ($t =$

11.32, df = 316.16, $P < 0.0001$) (Figure 2.3). Mean length of age-3 Bull Trout captured during the autumn 2019 trapping season was larger than the mean length of age-3 Bull Trout captured during the 2020 autumn trapping season ($t = 6.02$, df = 4.73, $P < 0.01$) (Figure 2.3). The mean length of spring out-migrating Bull Trout could not be directly compared to other seasons; however, it is worth noting that all age-2 fish captured in the spring were larger than the minimum transport length of 120 mm (Figure 2.3).

In the East Fork Bull River, we were not able to construct a length-at-age key for the trapping seasons due to the lack of tagged and trapped out-migrants. Thus, age at out-migration data was limited to previously aged, out-migrating Bull Trout from the East Fork Bull River (Table 2.2). Although sample size was limited, out-migration occurred at age 2, age 3 and age 4 (Table 2.2). The total number of out-migrating Bull Trout could not be estimated because we could not quantify capture efficiency. Length-at-age could not be compared for Bull Trout captured in East Fork Bull River during trapping seasons. In East Fork Bull River, all captured Bull Trout were larger than the minimum transport length of 120 mm (Figure 2.4).

Timing of out-migration and overall efficiency of downstream trapping methods

In Graves Creek, out-migration primarily occurred in three discrete events, and out-migration events coincided with the trapping seasons (Figure 2.5). Three age-2 Bull Trout from the 2017 year-class, and eight age-1 Bull Trout from the 2018 year-class out-migrated prior to the autumn 2019 trapping season (Figure 2.5). During the autumn 2019 trapping season, age-2 Bull Trout primarily out-migrated throughout September and October; whereas, age-1 Bull Trout out-migration showed a defined peaked in late October and continued into November (Figure 2.5). In December 2019 and January 2020, three Bull Trout from the 2017 year-class, and one

Bull Trout from the 2018 year-class out-migrated. Just prior to the spring 2020 trapping season, four Bull Trout from the 2018 year-class out-migrated (Figure 2.5). A large pulse of age-2 Bull Trout from the 2018 year-class out-migrated in mid to late April, with few captured in the trap (Figure 2.5). None of the age-2 out-migrants in May 2020 through mid-June 2020 were captured by the trap (Figure 2.5). Seven Bull Trout out-migrated in July, three from the 2018 year-class and four from the 2019 year-class. In mid to late August, four Bull Trout from the 2018 year-class, and one Bull Trout from the 2019 year-class out-migrated (Figure 2.5). In autumn 2020, out-migration of age-2 Bull Trout occurred through September, October and November, and the majority were captured by the trap (Figure 2.5). One Bull Trout from the 2017 year-class out-migrated in September 2019, and four Bull Trout from the 2019 year-class out-migrated from late September to early November (Figure 2.5).

Three-hundred and eight of the 821 Bull Trout tagged in Graves Creek were confirmed to have out-migrated from July 2019 through November 2020 (Table 2.3). Fifty-six percent of out-migrating Bull Trout out-migrated during trapping seasons and were captured by the weir trap (Table 2.3). Thirty-four percent of the tagged out-migrants were missed during trapping seasons and of those, 18% were missed when the weir was partially fishing; 10% missed during holidays, weekends, or volitional passage days; and 6% were missed for unknown reasons (Table 2.3). Ten percent of the total number of tagged Bull Trout out-migrated during seasons when the trap was not fishing (Table 2.3). Age-1 Bull Trout were the most likely to be missed for unknown reasons (Table 2.3). Of the 221 age-2 out-migrants, 51% were captured, 41% were missed during trapping seasons, and 8% out-migrated during seasons when the trap was not fishing (Table 2.3).

Four tagged age-3 Bull Trout out-migrated, and two were captured in the trap, while two out-migrated during seasons that the trap was not fishing (Table 2.3).

In East Fork Bull River, 18 of the 144 tagged Bull Trout out-migrated. Seventeen of the 18 tagged out-migrants out-migrated during the trapping seasons; however, only one was captured (Figure 2.6). In autumn 2019, one Bull Trout out-migrated in late October, and one Bull Trout out-migrated in late November (Figure 2.6). One Bull Trout out-migrated prior to the spring 2020 trapping season, and one Bull Trout out-migrated during the spring trapping season (Figure 2.6). The majority of out-migration occurred from mid-September through November during the autumn 2020 trapping season (Figure 2.6).

Discussion

Our results indicated that the downstream trapping program in Graves Creek captured variation in age-at-out-migration, and timing of out-migration of juvenile Bull Trout during the autumn trapping seasons. Although the spring trapping season coincided with the timing of the spring out-migration event in Graves Creek, few spring out-migrating Bull Trout were successfully captured. Establishing a representative population of tagged fish in Graves Creek enabled the use the PIT-antennas to monitor out-migration year-round and highlighted how knowledge based on trap captures can be biased unless seasonal variability in capture efficiency is explicitly quantified. Identifying the factors that contribute to fish being missed by the trap (i.e., age, season of out-migration) enables management actions to address potential sources of selectivity in the program and maximize variation within the population of transported Bull Trout. Conserving variation within life-history strategies maximizes the chances of success for the downstream transport program and makes the Bull Trout populations more resilient in the future.

Seasonal variation in capture efficiency was substantial and likely contributed to a biased knowledge of juvenile Bull Trout out-migration dynamics in Graves Creek prior to this study. In other systems with adfluvial Bull Trout populations, juvenile out-migration has been observed to occur in two major peaks annually, once in the spring and once in the autumn (Hemmingsen et al. 2001; Downs et al. 2006; Ratliff et al. 2015). Prior to this study, only one major peak in out-migration was observed annually in Graves Creek based on trapping data and occurred in the autumn. Use of the PIT-antennas revealed major out-migration events from Graves Creek in the spring and autumn, and the spring out-migration event was likely previously masked by low capture efficiencies. Capture efficiencies in the spring were so low that even traditional methods to account for capture efficiency, such as releasing captured fish above the trap and determining the proportion recaptured (Volkhardt et al. 2007) would likely have failed to reflect the extent of the out-migration, given no tagged Bull Trout were trapped during the month of May. Density of Bull Trout in Graves Creek during the study duration was higher than historically observed in Graves Creek, and higher than densities of juvenile Bull Trout observed in direct tributaries to Lake Pend Oreille (Frawley et al. 2020). High densities may have influenced the magnitude of spring out-migration observed during this study; therefore, additional research over multiple trapping seasons is necessary to understand temporal variation in the magnitude of spring out-migration. Capture efficiency during the autumn trapping seasons was high overall. In the autumn trapping seasons, using the number of Bull Trout captured in the traps as a metric for total out-migration without accounting for capture efficiency would have underestimated total out-migration by 6 – 15% (based on 95% confidence intervals) in 2019 and 4 – 14% in 2020. In the spring, using the number of age-2 Bull Trout captured in the traps as a metric for total out-migration without accounting for capture efficiency would have underestimated total out-migration by 78 – 93%. Therefore, seasonal variability in capture efficiency caused variation in the discrepancy between the number of Bull Trout captured in the trap and the total number of out-migrating Bull Trout.

In salmonids, variation in migration timing represents an important evolutionary trait that allows populations to be more resilient to stochastic environmental events by spreading the risk of migration over a longer period of time (Schindler et al. 2010; Moore et al. 2014). Thus, if trap-and-haul programs limit trapping to certain seasons based on conditions, or desirability of certain fish, the program could be selecting against variable life-history timing (Kock et al. 2020). For example, if one were to trap spring out-migrating fish, but only following the peak in spring discharge, early out-migrating fish would be selected against. Over time, this could lead to a loss of diversity in out-migration timing, making the populations less resilient in the future (Kock et al. 2020). The duration of the trapping seasons appeared appropriate to capture the majority of out-migrating Bull Trout from Graves Creek. Of the total tagged out-migrating Bull Trout, only 10% were missed due to out of season out-migration. However, despite the spring trapping season coinciding with the spring out-migration event, low trap efficiencies, particularly in May, suggesting that spring out-migrating Bull Trout are potentially experiencing negative selection.

Several factors can influence capture efficiency of the permanent weir and increasing capture efficiency requires that these factors are identified. During the spring trapping season, most fish that were missed out-migrated when the trap was partially fishing due to poor trapping conditions (i.e., the trap was overtopped with water because of high flows and high debris loads). Efforts to improve spring capture efficiencies should focus on increasing the ability of the trap to remain fully fishing through high flows. In the autumn 2019 trapping season, the majority of fish were missed for unknown reasons, meaning the weir appeared to be fully fishing. Eleven out of 12 fish missed for unknown reasons were age 1. Given the skewed age-distribution, it is likely that the small age-1 Bull Trout were able to escape through gaps in or between weir panels on the trap. Capture efficiency for age-1 Bull Trout improved in autumn 2020, however; fewer age-1 Bull Trout out-migrated in the autumn of 2020, and only one Bull Trout less than 120 mm was captured in the trap in 2020, whereas 50 Bull Trout less than 120 mm were captured in autumn 2019. Therefore, the increased capture efficiency may have resulted from fewer small individuals out-migrating. Given that the minimum length to transport Bull Trout is 120 mm, size selectivity below this threshold will not influence the transport program, however, it is important to acknowledge when using the number of Bull Trout captured in the trap as a metric for total out-migration. The spacing on and between panels on the permanent weir was designed to minimize impingement while effectively capturing age-1 and older Bull Trout. Efforts to improve capture efficiency during the autumn trapping seasons should focus on minimizing potential spaces for escapement on the trap by adjusting the panel spacing or using netting to cover gaps.

The age-class structure of juvenile out-migrating Bull Trout can be variable among populations and can vary among years within a single population. In general, the majority of juvenile Bull Trout in adfluvial systems out-migrate between age 0 and age 3, with age-2 Bull Trout representing the majority of out-migrants, which was similar to what we observed in Graves Creek (Zymonas 2006; Downs et al. 2006). There is currently no evidence that Bull

Trout out-migrating at age 0 survive in a lacustrine environment (Downs et al. 2006; Zymonas 2006; Ratliffe et al. 2015), and we did not attempt to capture or enumerate age-0 Bull Trout. Despite variation in capture efficiency among ages during the autumn 2019 and autumn 2020 trapping seasons, the age-class structure of captured Bull Trout was reflective of the age-class structure of all out-migrating Bull Trout (indicated by the total number of out-migrants calculation). Therefore, we did not find evidence that the current autumn trapping methods were selecting against variation in age-at-out-migration. In the spring, we were only able to quantify out-migration of age-2 Bull Trout. We were limited to one year of spring trapping data due to the timeline of the study, thus it is unknown to what degree the age structure of spring out-migrating Bull Trout varies by year. However, the two age-1 Bull Trout captured in the trap during the spring did not meet the minimum length for transport (120 mm), therefore spring trapping and transport efforts will likely continue to focus on age-2 and older Bull Trout.

The seasonal capture efficiencies in Graves Creek have implications for Bull Trout that use the reservoir system as a surrogate for lake habitat (hereafter “reservoir-type”). Although the success (where success is defined as the probability of an out-migrating Bull Trout surviving to maturity and returning to their natal stream to spawn) of reservoir-type Bull Trout is hypothesized to be lower than Bull Trout transported to Pend Oreille, past studies have found that reservoir-type fish do contribute to the Bull Trout population in Graves Creek (DeHaan and Bernall 2013). Variation in life-history strategies is common in Bull Trout populations (Rieman and Mclntyre 1993; Al-Chokhachy and Budy 2008; Howell et al. 2016). Thus, while the reservoir-type life history strategy is not natural, homogenizing the life-history strategies in the populations by transporting all out-migrating Bull Trout may also be unnatural. Due to the high degree of human intervention involved in two-way trap-and-haul program, there is ongoing potential that the success of the program could unexpectedly vary because of mechanical failures or human errors. Even with potentially lower survival rates, reservoir-type fish may serve as an important buffer to variation in success of the two-way trap-and-haul program. However, it is possible that with increasing water temperatures and increased abundance of piscivorous non-native species, over time the reservoir system could begin to act as an ecological sink where Bull Trout that attempt to grow to maturity experience little to no survival and are essentially losses to the population (Schlaepfer et al. 2002). With investments into infrastructure enabling the use of full-capture traps such as the permanent weir, rather than partial capture traps such as rotary screw traps, decisions will need to be made regarding whether a proportion of fish should be allowed to enter the reservoir or all fish should be transported. Given the management implications, it is vital that the relative success of the reservoir-type Bull Trout be evaluated. Prior to this study it was unknown how many Bull Trout were entering the reservoir system, when they were entering the reservoir, and the age of the fish entering the reservoir. We found that autumn out-migrating Bull Trout are better represented in the transport program, whereas spring out-migrating Bull Trout are better represented in the reservoir system, where they may mature in the reservoirs or migrate volitionally downstream to Lake Pend Oreille. The number of tagged Bull Trout that out-migrated at age-2 over the course of the study that were captured was nearly equal to the number of age-2 out-migrating Bull Trout that entered the reservoir; however, the majority of age-2 Bull Trout that entered the reservoir entered during the spring, thus they have a smaller body size relative to fall age-2 out-migrants that have an additional summer to grow. Timing of out-migration and size-at-out-migration have been identified as factors that influence the probability that Bull Trout will survive to maturity (Oldenburg 2017). Therefore, the information we collected will enable future efforts to compare the relative success of reservoir-type Bull Trout, volitional Lake Pend Oreille out-migrants, and transported Bull Trout, while accounting for underlying factors that may influence survival based on characteristics of the Bull Trout that contribute to each life-history strategy.

In the East Fork Bull River, we were not able to quantify capture efficiency or estimate the true magnitude and age-class structure of out-migration. Without an understanding of potential size selectivity in the traps, it is difficult to determine how size-selectivity of the traps may be biasing the current understanding of the out-migration dynamics in the East Fork Bull River. Moving forward, resources should focus on improving trap capture efficiencies in the East Fork Bull. Given the current state of the traps, attempts to quantify capture efficiencies using PIT-tagged fish will likely fail unless a greater number of bull trout can be tagged. Alternatively, capture efficiencies could be estimated using more traditional techniques, such as releasing tagged fish above the trap (Volkhardt et al. 2007). However, until capture efficiencies can be improved, this would likely result in the escapement of most potential transports as fish that are released upstream of the trap have a low probability of being recaptured.

Using stationary PIT-antennas to calculate capture efficiency and quantify out-migration of the trap had advantages and disadvantages when compared to the more traditional method of releasing fish above a trap to quantify capture efficiency (Volkhardt et al. 2007). Releasing fish upstream of a trap increases handling time, can influence out-migration behavior and timing, and leaves fish vulnerable to predation (Miller et al. 2000). For the trap-and-haul program, releasing captured fish means potentially losing fish that could have been transported if they are missed by the trap after being released. If the primary objective of calculating capture efficiency is to understand potential biases in capture efficiency, using PIT-antennas may be advantageous because the traditional method evaluates efficiency using fish that were captured in the trap at least once. Using PIT-antennas requires that an adequate sample of fish can be tagged prior to out-migration and relies on the assumption that the tagged fish are representative of the population. Determining how much sampling effort is needed for a given stream may be difficult and would likely require trial-and-error. Additionally, using tagged fish means no control over the timing and conditions of capture efficiency trials, whereas releasing fish above the trap enables control of the sample size and trap efficiency can be evaluated for specific abiotic conditions.

An additional challenge presented by the use of PIT-antennas to quantify out-migration is determining how to classify fish as out-migrants based on detections, while considering variable detection probability. Multiple factors can influence detection probability of PIT antennas, including environmental conditions such as discharge or stage height, and characteristics or behaviors of the fish (Zydlewski et al. 2006). Placing multiple independent antennas or arrays in a stream can aid in the understanding of detection probability and enable direction of movement to be determined (Zydlewski et al. 2006; Connolly et al. 2008). While calculations of detection probability of the PIT antennas in Graves Creek have indicated a high probability of detection on at least one antenna (> 0.97), the detection probability of each individual antenna varied, particularly at high flows (E. W. Oldenburg, unpublished data). We chose a semi-conservative approach to classifying out-migration by considering fish as out-migrants if they were detected on at least one antenna downstream of the trap, or captured in the trap. While this protocol included a greater number of fish than if our protocol required directionality (i.e., detection on one upstream and one downstream antenna), the protocol excluded several fish (n=13) that were only detected on an antenna located upstream of the trap in the spring. Further investigation into the factors that influence detection probability of each antenna on Graves Creek could enable condition specific protocols and the ability to directly quantify seasonal variation in detection probability.

Overall, our assessment of the downstream trapping efforts in Graves Creek indicated that Bull Trout transported during the autumn out-migration periods generally reflect the natural out-migration dynamics of the population. We also found that the current trapping seasons occur within the time periods of the major out-migration events, indicating little concern for selectivity against Bull Trout that may out-migrate outside of these time periods. However, the low capture efficiencies in the spring suggest that a disproportionate number of the spring out-migrants are not transported. Depending on the relative success of fish that are not transported, spring out-migrating Bull Trout may experience negative selection over time. Research into the demographic and genetic characteristics of spring out-migrating Bull Trout across a longer duration of time is needed to understand the relative importance of this currently underrepresented group of out-migrants in the trap-and-haul program.

For thermally sensitive species such as Bull Trout, climate change will increase habitat fragmentation (Rieman et al. 2007; Isaak et al. 2015), thus it is important to identify solutions that can maintain connectivity between cold-water tributaries and thermal refugia such as large, natural lakes. Trap-and-haul programs can restore connectivity and conserve migratory life-history strategies in populations that are fragmented by physical and thermal barriers (Bunt et al.

2012; Silva et al. 2018; Harris et al. 2019). If trap-and-haul programs can reflect underlying, natural out-migration dynamics of populations, they can increase the resilience of Bull Trout populations in the future by maximizing variation in life-history strategies (Waldman et al. 2016). Our study highlighted how PIT-technology can be used to evaluate the efficacy of downstream trapping programs in capturing variation in out-migration dynamics. In systems where trap-and-haul programs are being considered, PIT-technology can provide insight into the amount and timing of trapping effort necessary to capture natural variation in out-migration dynamics and thus, maximize the resiliency of populations.

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Tables

Table 2.1. Capture efficiency and number of out-migrating Bull Trout from Graves Creek during the autumn 2019 (4 September 2019 – 27 November 2019), spring 2020 (15 April 2020 – 2 July 2020), and autumn 2020 (2 September 2020 – 20 November 2020) trapping seasons. Trapped fish are classified as previously tagged or not tagged, and missed fish are classified based on the reason for being missed. Capture efficiency of the permanent weir was calculated using fish missed for unknown reasons or when the trap was partially fishing; whereas, overall efficiency included all fish missed during the trapping season, and the number of out-migrants was estimated based on overall efficiency.

	Trapped		Missed							
Age (year-class)	Tagged	Not tagged	Unknown	Partial	Weekend / holiday	Volitional	Capture efficiency of permanent weir (%)	Overall capture efficiency (%)	Estimated number missed (95% C.I.)	Estimated number of out-migrants (95% C.I.)
Autumn 2019										
Age 1 (2018)	55	442	11	0	0	1	83	82	107 (62)	604 (62)
Age 2 (2017)	19	183	1	0	0	2	95	86	30 (34)	232 (34)
Age 3 (2016)	1	4	0	0	0	0	100	100	0	5
Total	75	629	12	0	0	3	93	89	136 (96)	841 (96)
Spring 2020										
Age 1 (2019)	-	2	-	-	-	-	-	-	-	2
Age 2 (2018)	9	41	5	52	20	0	14	10	393 (221)	443 (221)
Total	9	43	5	52	20	0	14	10	393 (221)	445 (221)
Autumn 2020										
Age 1 (2019)	4	71	0	0	0	0	100	100	0	75
Age 2 (2018)	85[a]	451[b]	1	2	3	4	97	89	62 (37)	598 (37)
Age 3 (2017)	1	4	0	0	0	0	100	100	0	5
Total	90[a]	526[b]	1	2	3	4	99	96	62 (37)	678 (37)

[a] Number includes Bull Trout that were captured in the trap, but subsequently removed due to Mink predation.

[b] Number includes 149 Bull Trout estimated to have been removed by Mink.

Table 2.2. Age-at-out-migration and number (N) of juvenile Bull Trout that were previously tagged and out-migrated from the East Fork Bull River during the autumn 2019, spring 2020, and autumn 2020 trapping seasons, and one fish that out-migrated prior to the spring 2020 trapping season (winter 2020).

Season (year)	Age-at-out-migration (year-class)	N
Autumn (2019)	2 (2017)	1
	3 (2016)	1
Winter (2020)	3 (2017)	1
Spring (2020)	4 (2016)	1
Autumn (2020)	2 (2018)	2
	3 (2017)	11
	4 (2016)	1

Table 2.3. Fate of tagged Bull Trout out-migrating from Graves Creek, Montana, from July 2019 – December 2020, with fates defined as captured in weir trap, missed (unknown reasons), missed (not fishing or partially fishing due to holiday, weekends, or volitional passage), missed (trap partially fishing due to conditions), or missed (not fishing for the season).

Age at out-migration (n)	Trapped	Missed unknown	Missed holiday / weekend / volitional	Missed Partial	Missed out of season
1 (83)	59	11	1	0	12
2 (221)	113	7	29	54	18
3 (4)	2	0	0	0	2
All ages (308)	174	18	30	54	32

Figures

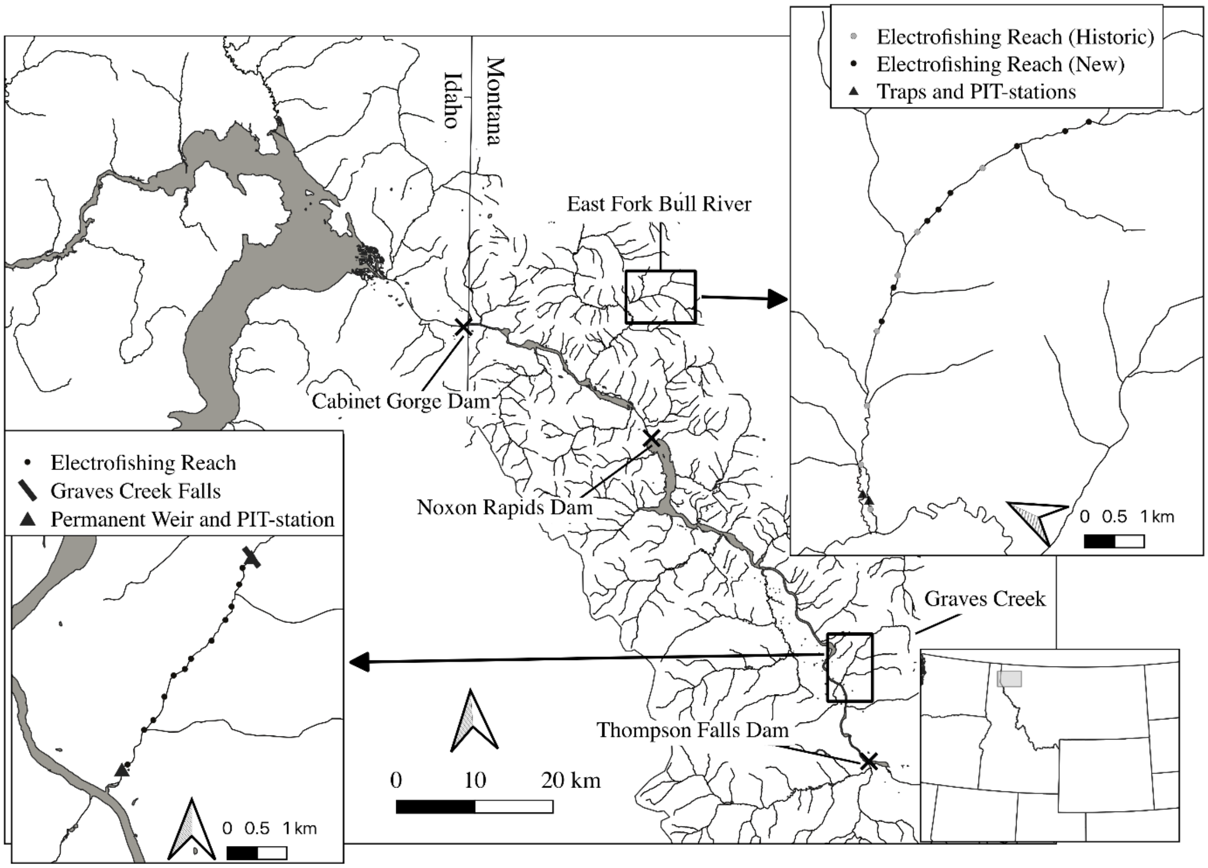

Figure 2.1. Lower Clark Fork River watershed in western Montana. Lower left inset map depicts the study area on Graves Creek, with the location of the sampling reaches. Upper right inset map depicts the study area on East Fork Bull River, with locations of sampling reaches. The lower right inset map depicts the location of the study in the states Idaho and Montana. Maps were created using QGIS 3.4.7, with layers from the USGS National Hydrography Dataset.

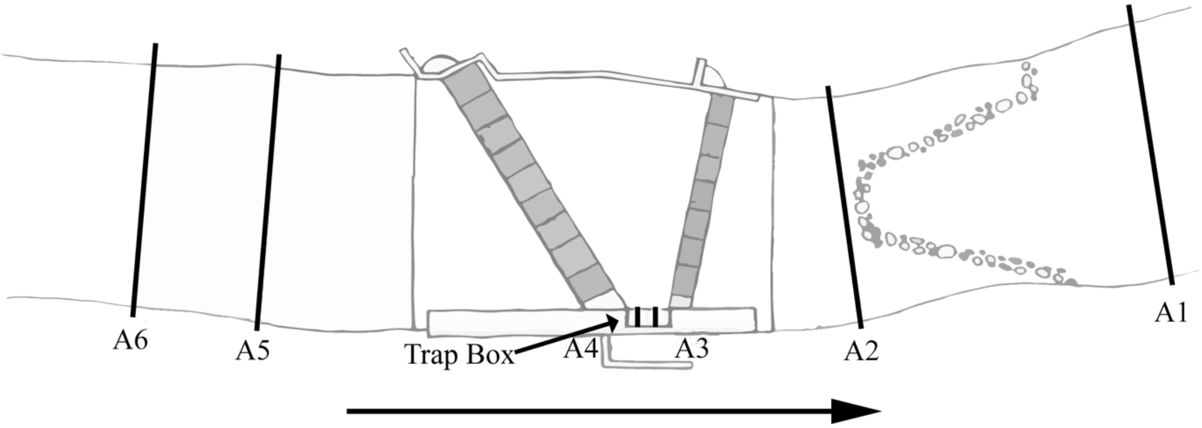

Figure 2.2. Diagram of the permanent weir and stationary PIT-antennas located at river kilometer 0.5 on Graves Creek, with arrow indicating direction of flow. The permanent weir trap was comprised of two rows of weir panels attached to a concrete slab. Antennas are depicted with an 'A' preceding the number, A6 and A5 are located upstream of the trap, A4 and A3 are located within the trap box, and A2 and A1 are located downstream of the trap.

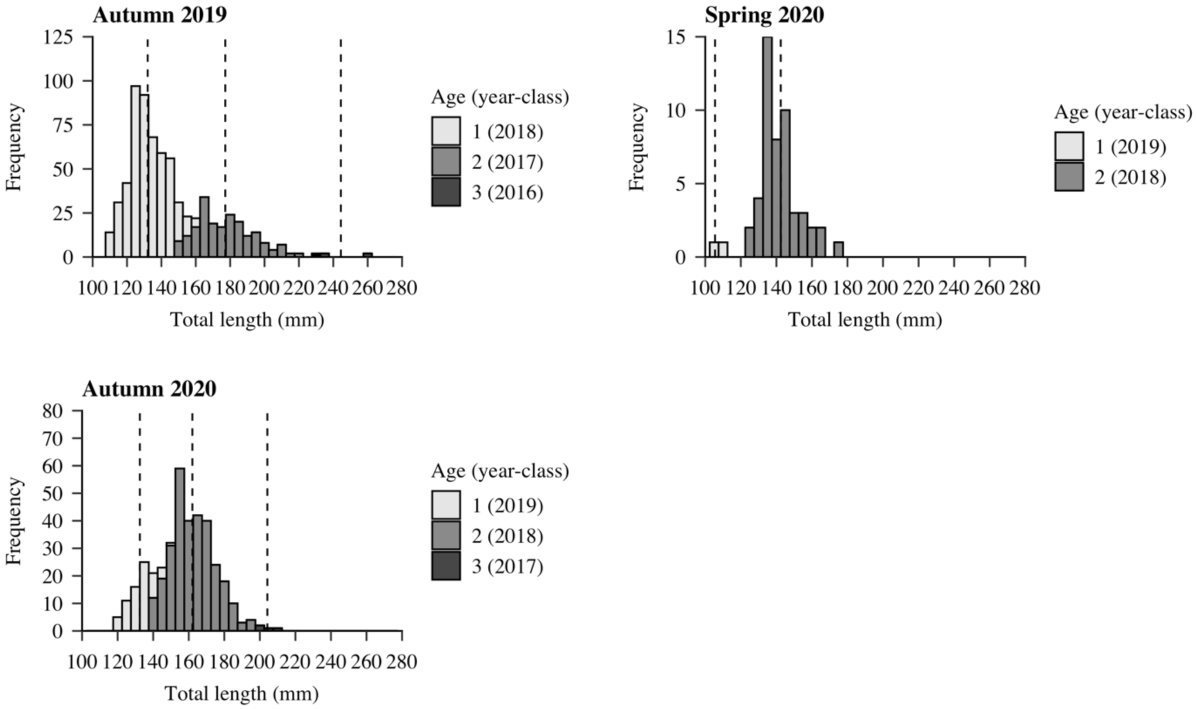

Figure 2.3. Length frequency of juvenile Bull Trout captured in permanent weir trap in Graves Creek, Montana during trapping seasons, autumn 2019 (4 September 2019 – 27 November 2019), spring 2020 (15 April 2020 – 2 July 2020), and autumn 2020 (2 September 2020 – 20 November 2020), with grey scale denoting age-class, and dotted lines delineating mean total length of the associated age-class.

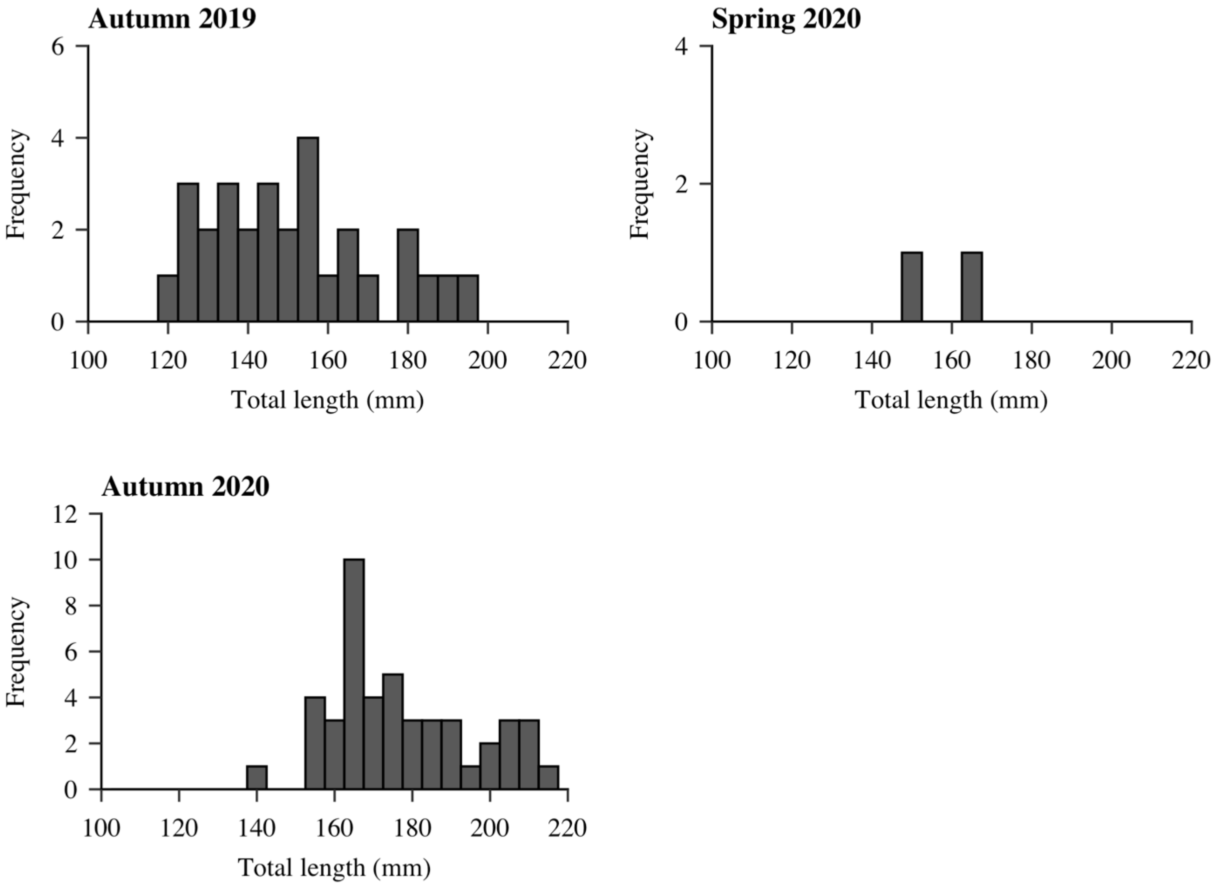

Figure 2.4. Length frequency of juvenile Bull Trout captured in traps in East Fork Bull River, Montana during trapping seasons, autumn 2019 (n=29) (4 September 2019 – 27 November 2019), spring 2020 (n=2) (15 April 2020 – 2 July 2020), and autumn 2020 (n=46) (2 September 2020 – 20 November 2020).

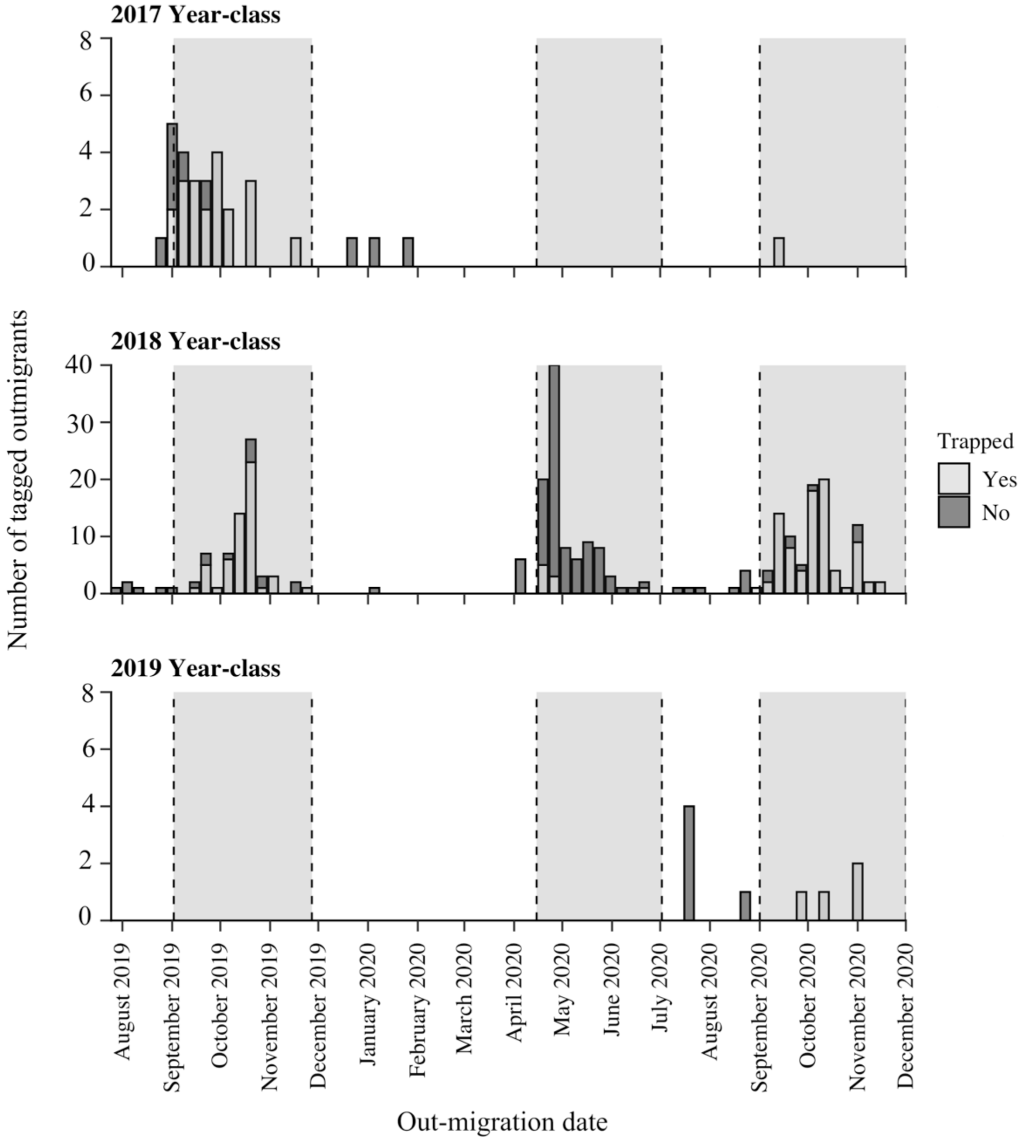

Figure 2.5. Timing distribution of tagged juvenile Bull Trout out-migrating from Graves Creek, Montana, by year-class, with dotted lines and shaded areas depicting trapping seasons, autumn 2019 (4 September 2019 – 27 November 2019), spring 2020 (15 April 2020 – 2 July 2020), and autumn 2020 (2 September 2020 – 20 November 2020). Grey scale within bars depicts whether a Bull Trout was captured in the trap (yes) or missed (no).

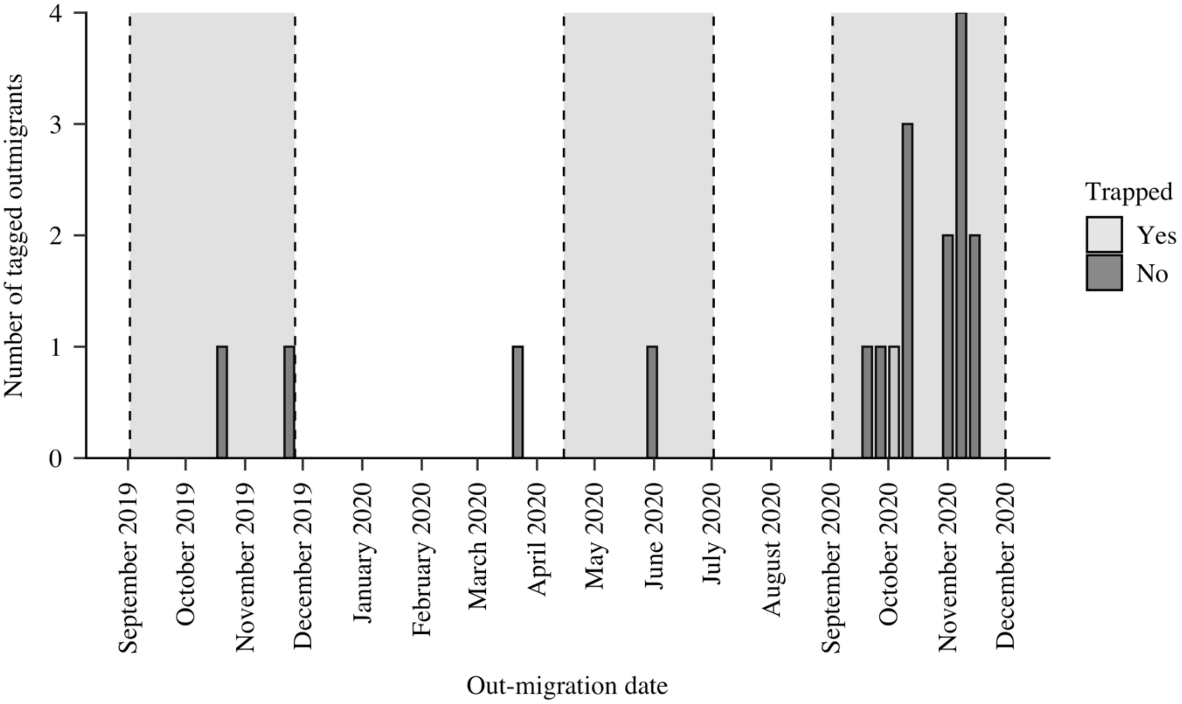

Figure 2.6. Timing distribution of tagged juvenile Bull Trout out-migrating from East Fork Bull River, Montana, with dotted lines and shaded areas depicting trapping seasons, autumn 2019 (4 September 2019 – 27 November 2019), spring 2020 (15 April 2020 – 2 July 2020), and autumn 2020 (2 September 2020 – 20 November 2020). Grey scale within bars depicts whether a Bull Trout was captured in the trap (yes) or missed (no).

CHAPTER THREE

INDIVIDUAL CHARACTERISTICS AND ABIOTIC FACTORS INFLUENCE OUT-MIGRATION DYNAMICS OF JUVENILE BULL TROUT

Contribution of Authors and Co-Authors

Manuscripts in Chapter 1, 2, and 3

Author: Madeline C. Lewis

Contributions: Conceived and implemented study, performed analyses, wrote the manuscript.

Co-Author: Christopher S. Guy

Contributions: Obtained funding, conceived study, assisted with implementation, discussed analyses and results, edited manuscript.

Co-Author: Eric W. Oldenburg

Contributions: Obtained funding, conceived study, assisted with implementation, discussed analyses and results, edited manuscript.

Co-Author: Thomas E. McMahon

Contributions: Assisted with planning, edited manuscript.

Manuscript Information

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Canadian Journal of Fisheries and Aquatic Sciences

Status of Manuscript:

__x__ Prepared for submission to a peer-reviewed journal

____ Officially submitted to a peer-reviewed journal

____ Accepted by a peer-reviewed journal

____ Published in a peer-reviewed journal

Abstract

Fragmentation of rivers through anthropogenic modifications poses an imminent threat to the persistence of migratory fish. Direct actions, such as trap-and-haul programs, will be necessary to restore and conserve the migratory life-history component in populations of partially migratory species such as bull trout *Salvelinus confluentus.* Trap-and-haul requires an understanding of the factors that contribute to a population producing out-migrants, as opposed to functioning as a resident population. We investigated factors that influenced the out-migration dynamics of juvenile bull trout in two tributaries to the lower Clark Fork River, Graves Creek and East Fork Bull River. Using a PIT-tag system, we tracked the out-migration of juvenile bull trout from summer of 2019 through autumn of 2020. In Graves Creek, the largest fish within a cohort were five times more likely to out-migrate at age-1 when compared to smaller fish within the cohort. The median time to out-migration for bull trout initially tagged at age-1 was 302 days for bull trout in the small size category (TL: 100-110 mm), 264 days for bull trout in the medium size category (TL: 111-118 mm), and 76 days for bull trout in the large category (TL: 119-138 mm). The median time to out-migration for bull trout initially tagged at age-2 was 46 days and did not vary based on individual characteristics. The magnitude of autumn out-migration appeared positively related to intra and inter-cohort densities. Our assessment of abiotic factors correlated with the magnitude of out-migration of bull trout during the three major out-migration events that occurred in Graves Creek during this study (autumn 2019, spring 2020, autumn 2020) indicated the strength of the relationship between abiotic factors and the magnitude of out-migrating bull trout was inconsistent among seasons, with pseudo-R^2 values varying from 0.14 to 0.62. Relative changes in abiotic factors, including discharge, water temperature, and

photoperiod, appeared to act as cues to out-migration, with the direction of change varying by season. These results highlight the complex interplay between individual characteristics, population dynamics, and environmental conditions, that lead to the production of out-migrants, and can be used to inform management actions to conserve the migratory component in bull trout populations.

Introduction

Migration is a common phenomenon observed in nature, exhibited by a variety of species at varying ecological scales. While some species are obligate migrants (i.e., requiring migration to complete their life cycle), many species demonstrate partial migration (Chapman et al. 2011). Partial migration is the ability of a species or population to demonstrate both migratory and resident life-history strategies (Chapman et al. 2011). For partially migratory species, migration represents a trade-off because migration is energetically costly; however, migration can allow individuals to maximize growth potential by exploiting a diversity of resources (Chapman et al. 2011, 2012). The presence of migratory individuals has substantial effects on the dynamics of ecosystems at multiple scales (Chapman et al. 2011, 2012) because migratory individuals can act as vectors to transport nutrients between habitats (Swanson et al. 2010), facilitate gene flow among populations (Rieman and Allendorf 2001), and repopulate areas in the event of a local extirpation (Morita and Yamamoto 2002).

Habitat fragmentation due to physical and thermal barriers has reduced connectivity among many freshwater habitats, to the detriment of migratory fishes (Tamario et al. 2019). The relative success of the migratory life-history strategy in populations can decrease or the migratory life-history component may be eliminated in the presence of barriers (Morita and Yamamoto 2002). Populations become dependent on resident fish to persist as the success of migration declines (Rieman et al. 1997; Rieman and Allendorf 2001; Branco et al. 2017). Resident populations are less resilient to stochasticity in the environment and become increasingly vulnerable to extirpation the longer they remain isolated (Dunham and Rieman 1999; Morita and Yamamoto 2002).

Bull trout *Salvelinus confluentus* are a species of char native to the northwestern United States and western Canada that exhibit a high degree of a plasticity in life-history strategies (Rieman and Mclntyre 1993). Bull trout may be resident or migratory and life-history strategies can vary within and among populations (Rieman and Mclntyre 1993; Al-Chokhachy and Budy 2008; Howell et al. 2016). Variation in life-history strategies is thought to be an evolutionary adaption to allow the species to persist in variable environments (Rieman and Mclntyre 1993; Dunham and Rieman 1999). Formerly large, interconnected bodies of water vital to the persistence of bull trout have become increasingly fragmented as a result of physical and thermal barriers (Rieman et al. 1997; Rieman and Allendorf 2001). Fragmentation of habitats has led to declines and losses of the migratory life-history strategy in some populations (Rieman et al. 1997; Rieman and Allendorf 2001). Climate change is likely to further the fragmentation of large habitat areas inhabited by bull trout (Rieman et al. 2007; Al-Chokhachy et al. 2016).

Conserving the migratory life-history strategy in bull trout populations is considered a key component to ensuring long-term persistence of the species (USFWS 2015). However, as connectivity in watersheds continues to decline, management actions requiring an increased degree of human intervention may be necessary to conserve migratory bull trout by ensuring connectivity between natal streams and cold-water refuges. Examples of management actions include trap-and-haul programs (Neraas and Spruell 2001; DeHaan and Bernall 2013) where connectivity is maintained by physically transporting bull trout between natal streams and cold-water refuges, and translocations, where bull trout may be introduced into formerly uninhabited habitat areas that remain connected and undisturbed (Galloway et al. 2016). In some cases, the success of management actions hinges on the ability to restore the migratory life-history strategy in bull trout populations where it has been eliminated. Transporting resident bull trout could lead to lower return rates, and removing resident individuals may be detrimental to source populations (Al-Chokhachy et al. 2015). Thus, there is a need to understand the factors that ultimately lead to a population of bull trout producing out-migrants (i.e., a number of juvenile bull trout that can be captured actively out-migrating from a stream).

Migration of fish has been described as a behavioral response to adversity (Thorpe 1988, 1994). However, a complex interplay of genetic, physiological, and environmental cues may influence out-migration decisions (Chapman et al. 2011, 2012). Interspecific and intraspecific competition for resources, predator-prey dynamics, and seasonal resource availability can cause variability in the magnitude of out-migration (Dermond et al., 2019; Dodson et al., 2013; Paul et al., 2000). In this study, we sought to answer the following questions to identify biotic and abiotic factors that influenced the out-migration dynamics of juvenile bull trout: 1) how do individual characteristics of a fish, and inter-cohort and intra-cohort densities, relate to age-at-out-migration, magnitude of out-migration, and timing of out-migration; 2) are abiotic factors (i.e., water temperature, discharge, and photoperiod) related to the magnitude of out-migration of juvenile bull trout during out-migration events; and 3) is relative change in water temperature, discharge, and photoperiod related to peaks in out-migration? Identifying biological characteristics of out-migrating bull trout, and abiotic factors that correlate with out-migration, can improve our understanding of the underlying mechanisms that ultimately lead a population to adopt a migratory life-history strategy.

Methods

Study area

The Clark Fork River originates near Butte, Montana, and flows in a northwest direction through western Montana before reaching Lake Pend Oreille, Idaho. The lower Clark Fork River is altered by a series of hydropower dams and reservoirs (Figure 3.1). Beginning in the early 2000s, a two-way trap-and-haul program was implemented to restore connectivity between local bull trout populations in tributaries to the lower Clark Fork River and Lake Pend Oreille. Recent investments in infrastructure to better monitor the out-migration dynamics of juvenile bull trout in tributaries within the trap-and-haul program has allowed for the monitoring of out-migration year-round using PIT-antennas. For this study, we focused on two of the primary streams within the trap-and-haul program, Graves Creek and East Fork Bull River.

Graves Creek enters the north side of Noxon Reservoir as a fourth order stream with a length of about 21 km. Graves Creek Falls is a natural barrier to upstream fish passage located at river kilometer 5.2, and bull trout distribution is limited to below the falls (Figure 3.1). Despite the small area of habitat occupied by bull trout, Graves Creek has consistently contributed a large proportion of transports to the downstream program (DeHaan and Bernall 2013). Bull trout and westslope cutthroat trout *Oncorhynchus clarkii lewisi,* are the most predominant species present below Graves Creek Falls (Horn and Tholl 2011). The habitat in Graves Creek below Graves Creek Falls is primarily classified as pool-riffle stream type, with small sections of higher gradient step-pools (River Design Group Inc 2005). The Graves Creek watershed is encompassed by a mix of private and public land ownership (River Design Group Inc 2005).

East Fork Bull River is about 13-km long and enters the Bull River as a fourth order stream (Figure 3.1). Near the confluence with the Bull River, the East Fork Bull River splits into a north channel and a south channel, which remain separated at the confluence with the Bull

River (Figure 3.1). The species assemblage in East Fork Bull River varies longitudinally. The upper reaches are primarily inhabited by bull trout and westslope cutthroat trout, whereas the lower reaches of East Fork Bull River have an increased density of non-native species, including rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, and brook trout *Salvelinus fontinalis* (Horn and Tholl 2011). The upper reaches of East Fork Bull River are primarily step-pool habitat, transitioning to a braided habitat type in the lower reaches (Land and Water Consulting Inc 2001). The East Fork Bull River primarily flows through public land, with a small portion of private land ownership in the lower reaches (Land and Water Consulting Inc 2001).

Sampling and abundance estimates

Juvenile bull trout were sampled at 12 100-m reaches in Graves Creek, and 15 100-m reaches in East Fork Bull River during the summer of 2019 and 2020 (Figure 3.1). A backpack electrofisher (Smith-Root, LR-24 model) was used in a downstream direction. All fish sampled were measured for total length (mm), weight (g), and scanned for the presence of a PIT (Passive Integrated Transponder) tag. If a PIT tag was not detected, bull trout > 100 mm received a 12-mm full duplex PIT tag. Prior to tag insertion, bull trout were anesthetized with 60 – 100 mg/L of MS-222 or Aqui-S. A disinfected needle or Biomark MK25 injector was used to insert the PIT tag into the anterior dorsal sinus of the bull trout. Bull trout were returned to live cars and once recovered, were released throughout the sampling reach. We tagged 821 juvenile bull trout in Graves Creek and 144 bull trout in East Fork Bull River. Age of sampled bull trout was determined by removing scales from the area above the lateral line ventral to the leading edge of the dorsal fins using a clean knife. A subset of scales was aged and were used to construct a length-at-age key using the ‘FSA’ package in R (Ogle et al. 2020). The length-at-age key was used to assign ages to all bull trout sampled, following methods outlined by Isermann and Knight (2005). Year-class was assigned based on the year that the bull trout hatched (i.e., redds in the autumn of 2017 resulted in the 2018 year-class), to enable tracking of cohorts through time.

Abundance at each electrofishing reach was estimated using a relationship derived from historic data collected from 2002 through 2018 as part of long-term monitoring in Graves Creek and East Fork Bull River. Abundance estimates from historic multi-pass depletion surveys were calculated using the Zippin K-pass removal estimate with the FSA package in R (Ogle et al. 2020) — surveys with a capture probability of < 0.5 were removed to avoid bias associated with low capture probabilities (Riley and Fausch 1992). First pass capture numbers and subsequent abundance estimates for each survey were plotted and a linear regression model was fit to the data collected on each stream. A standardized residual cut-off of ± 3 was used to eliminate outliers. Models for Graves Creek and East Fork Bull River indicated strong evidence for a relationship between the number of bull trout sampled on the first pass of a multi-pass depletion survey and the population estimate produced from that survey (Graves Creek: β_0 : -0.611, β_1 : 1.249, r^2 =0.97, P= < 0.0001, East Fork Bull: β_0 : 0.640, β_1 : 1.070, r^2 = 0.97, P <0 .0001). Thus, data from the first pass was used to predict the abundance in each reach where single-pass electrofishing was used. High and low abundance estimates were based on the 95% prediction intervals from the linear model. Density (number per m^2) was calculated for each reach and each year-class by reach and was the quotient from abundance and wetted area of the reach.

Monitoring out-migration

In Graves Creek, out-migration was monitored using a stationary PIT-monitoring station located at river kilometer 0.5 (Figure 3.1). The stationary PIT-monitoring station consists of four full-span antennas that are operated year-round, two upstream of the trap, two downstream of the trap, and two antennas that are integrated into the permanent weir trap. The permanent weir was constructed to capture juvenile bull trout for the trap-and-haul program, and two antennas within the trap operate when the trap is in use (September – late November and April – early July). Bull trout were considered out-migrants if detected on at least one antenna downstream of the trap, with out-migration date considered as the last date that the fish was detected.

In East Fork Bull River, two PIT-monitoring stations are present, consisting of two full span antennas in the north channel, and two full-span antennas in the south channel (Figure 3.1). The antennas in East Fork Bull River operate year-round. Bull trout were considered out-migrants if detected on any of the antennas in the East Fork Bull River. Low sample size of out-migrating bull trout limited the analyses for East Fork Bull River to the analysis of density-dependent out-migration, and the analysis of abiotic factors as potential cues to out-migration.

Abiotic factors

Water temperature data were collected from temperature loggers (OnSet HOBO TidbiT V2) placed in each electrofishing reach that recorded water temperature (°C) at 30-minute intervals. Discharge data (m^3/s) were collected at a stream gauging site located near the permanent weir trap in Graves Creek, and the trapping sites in East Fork Bull River. Photoperiod was estimated for the appropriate latitude and dates using the ‘geosphere’ package in R (Hijmans 2020).

Individual characteristics influencing age and timing of out-migration

Time-to-event analysis was used to evaluate whether individual characteristics of a bull trout were related with time to out-migration. Time-to-event analysis was implemented using bull trout from the 2018 year-class, initially encountered at age 1 in 2019, and bull trout from the 2017 year-class, initially encountered at age 2. The sample for the analysis only consisted of bull trout that out-migrated during the study. We did not include tagged fish that did not out-migrate because we could not discern whether the fish were mortalities or remained in the stream.

Three variables (i.e., length, relative condition, density) were selected based on prior hypothesis regarding bull trout out-migration. Length at the time of summer electrofishing was included and used as a surrogate of growth rate. Relative condition factor (K_n; Neumann et al. 2012) was calculated and included as an index to body condition. Density of bull trout was estimated for each reach (see above). The Kaplan-Meier product limit method, a non-parametric maximum likelihood step function that evaluates the probability of an event occurring (in our case, out-migration) for a given group over time was used to evaluate the effects of each variable on time-to-out-migration (Kaplan and Meier 1958). To enable visualization of time-to-event curves, each variable was divided into three categories (quantiles of equal size) and fish were assigned into the categories (Table 3.1). Kaplan-Meir curves were fit for each category within a variable using the 'survival' package in R (Therneau 2020; R Core Team 2020). A log-rank test was performed to determine whether curves differed by category (Therneau 2020).

Inter-annual variation in density and magnitude of out-migration by age class

To evaluate the potential for density-dependent out-migration, we assessed interannual variation in the year-class specific density of bull trout, and the number of out-migrating bull trout by year-class. In Graves Creek and East Fork Bull River, density is the mean overall density of each year-class during the summer sampling season, calculated as described above. The magnitude of out-migration by year-class and age was compared between the autumn out-migration events in 2019 (4 September 2019 – 27 November 2019) and in 2020 (2 September 2020 – 20 November 2020). Only bull trout that out-migrated during the autumn events were considered to facilitate comparisons between years.

Abiotic factors influencing magnitude of out-migration

In Graves Creek, we assessed the relationship between abiotic factors (i.e., mean daily water temperature, photoperiod, and maximum daily discharge) and magnitude of bull trout out-migration during major out-migration events. Data were grouped into three time periods to capture the major out-migration events: autumn 2019 (15 August 2019 – 15 December 2019), spring 2020 (30 March 2020– 5 July 2020) and autumn 2020 (15 August 2020 – 5 November 2020). Separate models were fit for each season because previous findings indicated that the effect of abiotic factors that influence out-migration of bull trout may vary seasonally (Downs et al. 2006; Homel and Budy 2008). Data were grouped into three-day time periods to lessen the number of zeros in the response variable. The sum of bull trout out-migrating over the three days was the response variable, and the three-day mean of abiotic factors were the independent variables. A three-day time period was selected as it effectively minimized zeros while still capturing variation in abiotic factors. Maximum discharge was natural log transformed in the spring models due to extreme values associated with spring run-off. A Pearson's correlation coefficient matrix was used to determine if there was collinearity between independent variables, where high collinearity was defined as ≥ 0.60 (Zuur et al. 2009). If predictor variables exhibited high collinearity, they were not used in models concurrently. A negative-binomial generalized linear model (GLM) was implemented using the 'MASS' package in R to model the effects of environmental factors on the count of bull trout out-migrating (Ripley et al. 2020; R Core Team 2020). The negative binomial distribution was selected because the response were over dispersed count data (Zuur et al. 2009). Data visualization indicated that the relationship between out-migration count and mean water temperature and maximum discharge may not be linear; thus, we implemented models with up to second order terms for each of the variables. Models were selected using a forward stepwise approach, and the final models for each season were selected based on AIC score and pseudo-R^2 (Zuur et al. 2009). Independent variables were not included in the final models if they did not independently converge with the response variable. Predicted values of the final models were plotted with the observed counts by season to visualize relationships.

Abiotic cues to out-migration

Changepoint analysis was implemented to assess whether changes in abiotic factors act as cues to juvenile bull trout out-migration in Graves Creek and East Fork Bull River. Changepoint analysis identifies the points in a time series where the statistical properties of the time series demonstrate a change (Killick et al. 2012). The 'changepoint' package in R was used to identify changepoints in the time series of abiotic factors, with the Pruned Exact Linear Time (PELT) method, with a minimum segment length of 30 days (Killick et al. 2012; Killick and Eckley 2014; R Core Team 2020). Water temperature data were summarized using the daily mean water temperature at a single reach within each stream. Reach 1, the downstream most reach, in Graves Creek and the historic reach 7 in East Fork Bull River were selected for water temperature data because these reaches allowed for the longest period of time to be included in the analysis

(Figure 3.1). Time series for each stream began 2-days after the temperature loggers were placed, which was 25 July 2019 for Graves Creek and 10 August 2019 for East Fork Bull River. Time series were created for mean daily water temperature, maximum daily discharge, and photoperiod. The time series of maximum discharge was natural log-transformed to reduce the skewness.

For water temperature and discharge, changepoints were based on the mean and variance, and for photoperiod, changepoints were based on the mean. Changepoints were subsequently plotted with the time series of bull trout out-migrating per day to examine whether the changepoints acted as potential cues to out-migration, as evidenced by changepoints preceding major out-migration events

Results

Biological characteristics influencing age and timing of out-migration

Length category at time of tagging influenced time-to-out-migration (log-rank test: $\chi^2 = 72.6$, df=2, $P < 0.001$) for bull trout from the 2018 year-class that were initially encountered at age-1 (n=214), with large fish more likely to out-migrate early in the study period (Figure 3.2). The median time to out-migration (defined as the point when probability of remaining in the stream = 0.5) for was 302 days for bull trout in the small category, 264 days for bull trout in the medium category, and 76 days for bull trout in the large category. By November 2019, bull trout in the small (length range (mm) = 100 – 110, n = 74) and medium (length range (mm) = 110 – 118, n = 70) length categories had a 75% probability of remaining in the stream; however, bull trout in the large (length range (mm) = 118 – 138, n = 70) category had less than 40% probability of remaining in the stream — indicating that they were more likely to out-migrate early at age 1

(Figure 3.2). By June 2020, bull trout in the small category were twice as likely to remain in the stream when compared to medium length bull trout, and large bull trout had a less than 5% probability of remaining in the stream (Figure 3.2). The discrepancy in probabilities continued into the autumn of 2020, with small bull trout having the greatest probability of remaining in the stream until the conclusion of the study in November 2020 (Figure 3.2). Time-to-out-migration did not vary based on density in the reach (log-rank test: $\chi^2 = 3.6$, df=2, $P = 0.16$) or on relative condition (log-rank test: $\chi^2 = 3.3$, df=2, $P=0.19$).

None of the categories for any variable (i.e., length, density, relative condition) predicted time to out-migration for juvenile bull trout from the 2017 year-class that were initially encountered at age 2 ($n = 30$) (length [log-rank test: $\chi^2 = 0.1$, df=2, $P=0.97$]; density [log-rank test: $\chi^2 = 3.5$, df=2, $P < 0.17$], condition [log-rank test: $\chi^2 = 0.2$, df=2, $P=0.92$]). The median time-to-out-migration for bull trout from the 2017 year-class was 46 days. The probability of bull trout remaining in the stream following autumn 2019 was below 20% (Figure 3.3). A small number of bull trout from the 2017 year-class out-migrated at age 3 between the autumn 2019 and spring 2020 seasons, and the remaining fish out-migrated during the autumn 2020 season (Figure 3.3).

Inter-annual variation in density and magnitude of out-migration by age class

Overall mean density of juvenile bull trout in Graves Creek was higher in 2019 when compared to 2020 (Table 3.2). The proportion of autumn out-migrating bull trout that were age-1 varied considerably between the two autumn trapping seasons, from 74% in 2019 to 5% in 2020 (Table 3.2). In autumn of 2019, 90 bull trout out-migrated and 67 were age 1 from the 2018 year-class, 22 were age 2 from the 2017 year-class, with one fish from the 2016 year-class (Table 3.2). In autumn of 2020, 102 bull trout out-migrated and 5 were age-1 bull trout from the 2019 year-class, 96 were age-2 from the 2018 year-class, and one was age-3 (Table 3.2).

Overall mean density of juvenile bull trout in East Fork Bull River was higher in 2020 when compared to 2019, however, density was consistently lower than Graves Creek (Table 3.2). In East Fork Bull River, zero age-1 bull trout out-migrated. Two bull trout out-migrated in the autumn of 2019, one from the 2016 year-class and one from the 2017 year-class (Table 3.2). Number of out-migrating bull trout in the autumn of 2020 increased to 14, two were age 2 from the 2018 year-class, 11 were age 3 from the 2017 year-class, and one was age 4 from the 2016 year-class (Table 3.2).

Abiotic factors influencing magnitude of out-migration

In Graves Creek, the strength of the relationship between abiotic factors and the magnitude of out-migrating bull trout was inconsistent among seasons, with pseudo-R^2 values varying from 0.14 to 0.62 (Table 3.3). The magnitude of out-migration during the autumn of 2019 season was best explained by mean water temperature and maximum discharge (Table 3.3). Magnitude of out-migration had a curvilinear relationship with mean water temperature, peaking at 6.5 °C before declining as temperatures increased, and a positive relationship with discharge (Figure 3.4). The magnitude of out-migration during the spring 2020 had a curvilinear relationship with log maximum discharge, however, the model was only able to explain 14% of the variation in magnitude of out-migration (Table 3.3, Figure 3.4). During the autumn 2020 season, mean water temperature had a curvilinear relationship with magnitude of out-migration, with a peak at 7 °C (Figure 3.4).

Abiotic cues to out-migration

Changepoints in natural log of maximum discharge, water temperature, and photoperiod preceded out-migration events in Graves Creek and East Fork Bull River with the direction of the changepoints varying by season. In Graves Creek, 12 changepoints were identified in the mean and variance of log-maximum discharge (Figure 3.5). In autumn 2019, out-migration was occurring as discharge was reaching base flows (Figure 3.5). In late October 2019, a small positive changepoint in discharge, increasing from a mean natural log-maximum discharge of -1.17 cms to -0.98 cms, preceded the largest peak in out-migration (Figure 3.5). Out-migration in April 2020 began as mean log-maximum discharge increased from -1.46 cms to 1.00 cms, and peaked immediately following a large positive changepoint from a mean of 1.00 cms to 1.60 cms (Figure 3.5). Out-migration continued through the peak in discharge and began to taper off as discharge declined in mid-June 2019 (Figure 3.5). In the autumn of 2020, steady out-migration began as discharge declined to a mean of -0.79 cms, and peaked once discharge reached -1.15 cms (Figure 3.5). In Graves Creek, nine changepoints in mean daily water temperature were identified (Figure 3.6). In autumn 2019, out-migration occurred prior to the first negative changepoints in water temperature (Figure 3.6). A large negative changepoint in water temperature occurred in late September 2019 and preceded the largest peak in out-migration, with mean water temperature dropping from 9.9 °C to 5.4 °C (Figure 3.6). Immediately following the peak in out-migration, mean water temperature dropped to 2.6 °C, and out-migration declined, with only a few out-migration events occurring in November and December 2019 (Figure 3.6). Mean water temperature remained near a 2.6 °C, with sporadic out-migration, until mid-March 2020 when mean water temperature increased to 4.2 °C, and out-migration began (Figure 3.6). Out-migration peaked as mean water temperature increased to 5.8 °C (Figure 3.6). Out-migration tapered off in mid-June as mean water temperatures increased to 7.9 °C. Similar to autumn 2019, out-migration began in autumn 2020 prior to the first negative changepoints in water temperature. Out-migration peaked following the first negative changepoint in mean water temperature, with mean water temperature declining from 10.1 °C to 8.4 °C, and another peak in out-migration occurred at the next negative changepoint, where mean water temperature declined to 5.1 °C (Figure 3.6). Ten changepoints were identified in the mean of photoperiod (Figure 3.7). Due to the smooth and cyclic nature of photoperiod, changepoints are evenly spaced other than in the intervals of summer and winter (Figure 3.7). In autumn 2019 and autumn 2020, out-migration was associated with negative changepoints in photoperiod; however, out-migration peaked in the autumn of 2019 later than in 2020 (Figure 3.7). In the spring, positive changepoints in photoperiod preceded out-migration; however, out-migration continued through the summer solstice (Figure 3.7).

In the East Fork Bull River, nine changepoints were observed in log-maximum discharge (Figure 3.8). In autumn 2019, a small positive changepoint in mean log-maximum discharge, from -1.12 cms to -0.85 cms preceded the out-migration of two tagged bull trout. In the spring of 2020, one bull trout out-migrated prior to the first changepoint in discharge, and one bull trout out-migrated during peak discharge (Figure 3.8). In autumn 2020, out-migration began after discharge had reached baseflows in September 2020, and subsequently increased from baseflows of -0.96 cms to a mean of -0.64 cms (Figure 3.8). Nine changepoints were observed in mean water temperature in East Fork Bull River (Figure 3.9). In autumn 2019, one bull trout out-migrated following a negative changepoint from a mean temperature of 10.3 °C to 5.0 °C, and one bull trout out-migrated when mean water temperature declined again to 2.8 °C (Figure 3.9). A single bull trout out-migrated during March 2020 at 1.7 °C, and one more bull trout out-migrated after two changepoints in mean water temperature, increasing to 3.7 °C (Figure 3.9). Out-migration began in autumn 2020 when water temperature declined from 10.3 °C to 9.0 °C, and continued as water temperature decreased to 5.2 °C (Figure 3.10). Negative changepoints in photoperiod preceded out-migration in the autumn, and positive changepoint in photoperiod preceded out-migration in the spring (Figure 3.10).

Discussion

Variation in the influence of individual characteristics, population density, and abiotic factors indicate that multiple interrelated processes interact to influence variation in out-migration dynamics of juvenile bull trout. Age at out-migration was influenced by individual characteristics of bull trout and population density; however, this relationship was only observed in bull trout tagged at age 1. Magnitude of out-migration was influenced by maximum discharge and mean water temperature; however, neither abiotic factor was present in all three models. Changes in abiotic factors preceded the initiation of out-migration events and peaks in out-migration during out-migration event, with the direction of change varying based on the season.

At the individual level, length (surrogate for growth rate) influenced time to out-migration for bull trout initially tagged at age 1 in Graves Creek. The relationship between growth and migration has been studied in anadromous, fluvial, and adfluvial salmonids (Metcalfe et al. 1989; Gross 1991; Økland et al. 1993; Forseth et al. 1999; Heim et al. 2016). It is hypothesized that migration is a behavioral response to a lack of resources needed to reach maturity in natal streams with limited resources and low productivity (Thorpe 1994). Within migratory populations of salmonids, growth rate can influence the age or size when a fish will out-migrate (Metcalfe et al. 1989; Forseth et al. 1999; Heim et al. 2016). A high metabolic rate associated with fast growth may result in faster-growing individuals becoming energetically limited earlier in life than slower growing conspecifics, causing fast-growing fish to out-migrate and seek more abundant resources at a younger age and smaller size than slower growing fish in the same cohort (ØKland et al. 1993; Forseth et al. 1999; Heim et al. 2016). A lower metabolic rate may enable fish to remain in their natal stream longer, allowing slow-growing fish to reach a larger size before out-migrating with less risk (Økland et al. 1993; Thorpe 1994; Forseth et al. 1999).

Our results supported the hypothesis that faster growing fish are more likely to out-migrate from the stream at a younger age. The smallest bull trout were the most likely to remain in Graves Creek until the autumn when they were age 2, and the largest were the most likely to out-migrate at age 1. However, we found that the magnitude of the effect that growth rate may have on age-at-out-migration is likely mediated by other factors, such as density. Although we did not find that reach specific density influenced time-to-out-migration, the magnitude of out-migration at age 1 did appear to be related to overall density of the population. Overall density of bull trout in Graves Creek in 2019 was higher than in 2020, and the magnitude of age-1 bull trout out-migrating from Graves Creek was considerably higher in 2019 compared to 2020. At high densities, both intercohort and intracohort competition may exacerbate the energetic limits of fast-growing age-1 fish, leading to increased out-migration at age 1. For the 2017 year-class of bull trout in Graves Creek, that were initially encountered in the summer of 2019 at age 2, we did not identify any biological factors that related to time to out-migration. The majority of out-migration occurred in the autumn, with a small number remaining in the stream to reach age 3. The out-migration of age-2 bull trout regardless of individual characteristics supports what has been found in other adfluvial bull trout populations, where the magnitude of age-1 out-migration was positively related with density of bull trout in a stream, whereas out-migration for age-2 and older bull trout was consistently high and not correlated with density (Paul et al. 2000; Ratliff et al. 2015). In small, habitat limited streams such as Graves Creek, it is likely that once bull trout reach a certain age or size (age 2 in Graves Creek) migration becomes obligatory regardless of individual characteristics. The exact age or size of bull trout when migration becomes obligatory likely varies among streams and temporally within streams as conditions change (e.g., resource availability or density).

Additional support for the hypothesis of density driven out-migration was found in East Fork Bull River. Although densities and out-migration numbers were much lower than in Graves Creek, we observed a higher rate of out-migration from the East Fork Bull River in 2020 than in 2019, in conjunction with an overall increase in density in the stream. Additionally, most of the out-migrants from the East Fork Bull River were from the strong 2017 year-class, which suggests that intracohort competition contributes to the production of out-migrants. The older average age-at-out-migration from the East Fork Bull River may be a result of the overall low densities in East Fork Bull River, which would enable bull trout to remain in the stream for a longer time before becoming obligate migrants.

Although density may be a common and easily observed driver of early out-migration, the above evidence indicates that fundamentally, out-migration may be driven by a demand for resources (e.g., food, territory) that exceeds the supply in the stream (Thorpe 1994). Thus, even at low densities, it is plausible that any mechanism that reduces the supply of resources may lead to a greater majority of fish out-migrating at a young age. The mechanism could be a stochastic environmental event (e.g., drought), or a long-term trend that reduces available habitat or resources (e.g., increasing stream temperatures). There is evidence that bull trout that out-migrate at a younger age will have reduced survival probabilities, both within the transport program (Oldenburg 2017) and in natural populations (Paul et al. 2000b; Zymonas 2006; Downs et al. 2006; Ratliff et al. 2015). Given the survival implications, it is imperative that natural resource agencies continue to monitor populations to discern the cause of early out-migration.

Prior studies have observed that juvenile bull trout out-migration tends to correlate with increasing flows in the spring and decreasing water temperatures in autumn (Hemmingsen et al. 2001; Downs et al. 2006; Homel and Budy 2008; Ratliff et al. 2015). Other than a positive relationship between discharge and out-migration during autumn 2019 (similar to that observed by Homel and Budy (2008)) we found curvilinear relationships between the magnitude of out-migrating bull trout and abiotic factors. The inherent seasonality of abiotic factors and the temporal distribution of out-migration from Graves Creek make it difficult discern whether the non-linear relationships observed are a result of a causative relationship. An additional challenge associated with fitting models to understand the influence that abiotic factors have on magnitude of out-migration is that the relationship between out-migrating bull trout and abiotic factors may change throughout a season. Changes in abiotic factors can act as cues to begin out-migration; however, once all ‘eligible’ out-migrants have out-migrated, migration may decline even if the abiotic conditions remain the same (Spence and Dick 2014).

The changepoint analysis in conjunction with the non-linear relationships from the GLM models indicate that relative changes in abiotic conditions may act as cues to out-migration. While some changes may act as cues to initiate migration, others may represent conditions that are selected for after out-migration has been initiated. For example, although out-migration began as discharge declined in the autumn, small, positive changepoints in discharge in the autumn preceded peaks in out-migration. Changing abiotic factors during the spring and autumn may create periods where the supply and demand for resources is mismatched in the stream, leading to increased out-migration. We found that positive changepoints in water temperature in the spring preceded the initiation of the spring out-migration event. As ectotherms, the metabolism and energetic demands of salmonids are highly influenced by water temperature (Enders and Boisclair 2016). As water temperature increases from winter to spring, salmonids can experience a significant increase in metabolic rate and growth (Morgan et al. 2001). If productivity and food availability in a stream increase at a rate that is slower than the increase in the energetic demands of bull trout, out-migration may be initiated. In other migratory salmonids, the proportion of smolts in the spring was related to food availability and fish size, with large fish that experienced reduced feed rations being the most likely to begin smolting (indicating out-migration) (Jones et al. 2015). The proportion of smolts declined with increased food availability, and smaller fish were less likely to smolt (Jones et al. 2015), indicating support that energetic demand was the mechanism for spring out-migration. However, lab studies have indicated that increasing water temperature alone may not lead to smolting, rather an interaction between increasing water temperature and changing photoperiod explains spring out-migration (Muir et al. 1994; Bottengård and Jørgensen 2008). We found similar responses of bull trout out-migration to changepoints in time series of photoperiod and water temperature in the spring, however the correlation between water temperature and photoperiod makes it difficult to identify an interaction in a natural setting. A small positive changepoint in maximum discharge preceded the initial out-migration during the spring in Graves Creek, and out-migration peaked as the mean maximum spring discharge was reached. Past studies have indicated that the relationship between discharge and out-migration in the spring can vary among salmonid species and among populations of salmonids (Sykes et al. 2009; Spence and Dick 2014). In some populations of salmonids, increased discharge in the spring may act as a cue to out-migration (Sykes et al. 2009; Spence and Dick 2014). However, in other populations, increasing discharge appears to have a negative effect on out-migration and may act as a cue to cease out-migration (Sykes et al. 2009; Spence and Dick 2014). The lack of consistent relationship between increasing discharge and out-migration of salmonids in the spring may indicate that local adaptions influence how populations respond to abiotic cues (Spence and Dick 2014). Conversely, increased discharge may not be a primary cue to initiate spring out-migration and observed relationships may be a result of seasonal correlation (Sykes et al. 2009). Spring out-migration of juvenile bull trout occurs in the Metolius River which lacks a large spring peak in discharge due to groundwater influence, providing evidence that discharge may not be a primary cue to out-migrating for bull trout in the spring (Ratliff et al. 2015). If other abiotic factors such as water temperature have a stronger influence on out-migration timing in the spring than discharge, changing abiotic conditions could lead to out-migration occurring before or after peak discharge. Out-migrating during periods of high discharge may increase the survival of out-migrating bull trout by reducing energetic costs and decreasing migration times (Connor et al. 2003; Scheuerell et al.

2009); therefore, a mismatch in the timing of out-migration relative to peak discharge could potentially lead to lower survival rates of spring out-migrating bull trout.

In Graves Creek, negative changepoints in discharge preceded out-migration in the autumn. As discharge declines and approaches base flows in the autumn, the area of available habitat in streams is reduced. Although it would be expected that competition for habitat would result in smaller and less dominant fish out-migrating, the balance of survival in-stream over the winter and predation risk may explain why we observed the larger fish of a cohort out-migrating prior to winter (Dermond et al. 2019). As fish increase in size, they have increased energetic demands, making them more likely to starve in small headwater streams over winter, and they become less vulnerable to predators that may be encountered in larger, more productive environments (Dermond et al. 2019). Therefore, the risk from over wintering starvation in small, headwater streams may outweigh the risk of predation in larger, more productive environments (Dermond et al. 2019). Although out-migration began in the autumn following negative changepoints in discharge, a positive changepoint in discharge preceded the peaks in out-migration in the autumn 2019. Therefore, local increases in discharge may encourage out-migration by lessening the risks and energetic costs of migration (Connor et al. 2003; Scheuerell et al. 2009). In both summers in Graves Creek, out-migration began prior to the initial negative changepoints in water temperature. Out-migration preceding changepoints in water temperature indicates that water temperature may not be the primary cue to initiate out-migration in the autumn. However, as the season progressed, negative changepoints in water temperature did precede major out-migration events. Declining water temperatures and shortened photoperiods may act as a cue for bull trout to begin movements to overwintering habitat (Jakober et al. 1998).

Given the inherent seasonality of changing environmental conditions, and thus correlation among variables, it is difficult to understand the relative importance of each individual environmental cue in an uncontrolled natural setting. However, the relative importance and potential interaction among cues have implications for the conservation of migratory bull trout. As climate change alters thermal regimes, and human development continues to alter natural flow regimes, it will be vital to understand if and how migration cues may be altered. Further research into the biological characteristics and environmental cues to bull trout out-migration in a variety of streams, in conjunction with research conducted in controlled environment, will aid in furthering the understanding of what factors or combination of factors influence bull trout out-migration dynamics.

Our results highlight the complexity in the relationship between biological characteristics of individual bull trout, population dynamics, and abiotic factors that ultimately lead to out-migration. We found support for the hypothesis that out-migration of bull trout is driven by density-dependent processes (Johnston et al., 2007; Paul et al., 2000; Ratliff et al., 2015), which has implications for the restoration of the migratory life-history strategy in bull trout populations. If the migratory life-history strategy in a population becomes less successful (i.e., migratory adults begin to return at lower numbers or fail to return), densities will decline. As density declines, the demand for resources will be lowered, therefore remaining bull trout may begin to adopt a resident life-history strategy (Zymonas 2006). Due to lowered fecundity associated with smaller size-at-maturity, resident populations are likely to remain at low densities (Rieman and Mclntyre 1993). To restore the migratory life-history strategy, the density of the population would need to increase to a point at which demand for resources exceeds the supply of resources in a stream, initiating density-dependent out-migration. Increasing densities may require the translocation of large, fecund migratory adult bull trout, and active management actions such as trap-and-transport programs to ensure the continued existence of the migratory behavior of bull trout.

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Tables

Table 3.1. Variables and associated category values for the Kaplan-Meir analysis of time to out-migration for juvenile bull trout sampled from Graves Creek, Montana in the summer of 2018 and 2019 (sample size in parentheses).

		Year-class	
Variable	Category	2017	2018
Total length (mm)	Small	151 – 169 (11)	100 – 110 (74)
	Medium	170 – 181 (89)	111 – 118 (71)
	Large	182 – 201 (10)	119 – 138 (69)
Relative body condition (K_n)	Low	0.91 – 0.97 (10)	0.81 – 0.98 (72)
	Medium	0.98 – 0.99 (10)	0.99 – 1.02 (71)
	High	1.00 – 1.10 (10)	1.03 – 1.24 (71)
Density (number / m^2)	Low	0.009 – 0.065 (12)	0.009 – 0.068 (74)
	Medium	0.066 – 0.089 (10)	0.069 – 0.121 (91)
	High	0.090 – 0.146 (8)	0.122 – 0.146 (49)

Table 3.2. Summary of the sample population of bull trout in Graves Creek and East Fork Bull River, Montana, following electrofishing in the summer of 2019 and summer of 2020. Summer sampling numbers indicate total number of bull trout sampled, with the number of tagged bull trout in parenthesis. Density is the mean overall density of each year-class during the summer sampling season. Autumn out-migrants are tagged bull trout that out-migrated during the autumn out-migration events in 2019 (4 September 2019 – 27 November 2019) and in 2020 (2 September 2020 – 20 November 2020).

Age (year-class)	Summer sampling (N tagged)	Density (mean number / m^2) [95% P.I.])	Autumn out-migrants
Graves Creek 2019			
Age 1 (2018)	486 (451)	0.0701 (± 0.093)	67
Age 2 (2017)	37 (37)	0.059 (± 0.0011)	22
Age 3 (2016)	4 (4)	0.0007 (± 0.0001)	1
Total	527 (492)	0.0767 (± 0.0103)	90
Graves Creek 2020			
Age 1 (2019)	283 (251)	0.0418 (± 0.0075)	5
Age 2 (2018)	92 (90)	0.0138 (± 0.0024)	96
Age 3 (2017)	3 (3)	0.0005 (± 0.0001)	1
Total	378 (344)	0.0561 (± 0.0100)	102
East Fork Bull River 2019			
Age 1 (2018)	24 (24)	0.0027 (± 0.0009)	0
Age 2 (2017)	38 (37)	0.0041 (± 0.0015)	1
Age 3 (2016)	11 (11)	0.0011 (± 0.0005)	1
Age 4+	5 (5)	0.0006 (± 0.0004)	0
Total	78 (77)	0.0085 (±0.0033)	2
East Fork Bull River 2020			
Age 1 (2019)	31 (2)	0.0038 (± 0.0008)	0
Age 2 (2018)	17 (17)	0.0021 (± 0.0005)	2
Age 3 (2017)	43 (43)	0.0053 (±0.0017)	11
Age 4+	5 (5)	0.0006 (± 0.0002)	1
Total	96 (67)	0.0118 (± 0.0032)	14

Table 3.3. Summary of the top negative binomial generalized linear model with a log-link function by season, autumn 2019 (15 August 2019 – 15 December 2019), spring 2020 (30 March 2020– 5 July 2020), and autumn 2020 (15 August 2020 – 5 November 2020), modeling the relationship of abiotic factors, including mean water temperature (T [°C]) and maximum discharge (D [cubic meters per second]) to the number of out-migrating bull trout from Graves Creek, Montana, with all variables grouped into three-day time periods.

		Parameter Estimates					
Season	Model	ß$_0$	ß$_1$	ß$_2$	ß$_3$	Pseudo R^2	Residual d.f.
Autumn 2019	$\log(\text{count}) \sim \beta_0 + \beta_1(\text{T}) + \beta_2(\text{T})^2 + \beta_3(\text{D})$	-6.09 (1.14)	1.42 (0.34)	-0.11 (0.02)	9.53 (2.03)	0.62	37
Spring 2020	$\log(\text{count}) \sim \beta_0 + \beta_1(\log(\text{D})) + \beta_2(\log(\text{D}))^2$	0.86 (0.39)	0.96 (0.39)	-0.44 (0.19)	-	0.14	31
Autumn 2020	$\log(\text{count}) \sim \beta_0 + \beta_1(\text{T}) + \beta_2(\text{T})^2$	-8.10 (2.97)	2.80 (0.85)	-0.20 (0.06)	-	0.35	26

Figures

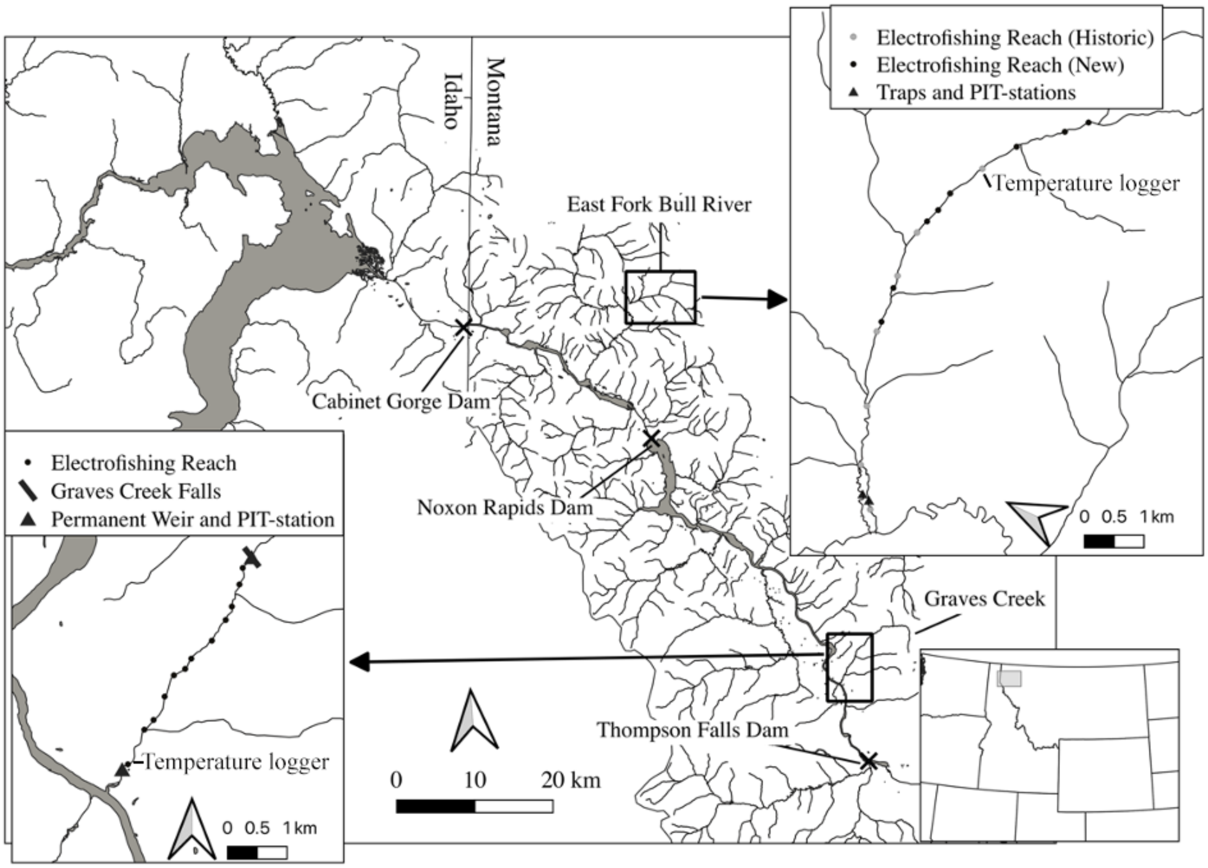

Figure 3.2. The lower Clark Fork River watershed, with the locations of the three hydropower dams labeled. The lower left inset map depicts the study area on Graves Creek, with the location of the sampling reaches. The upper right inset map depicts the East Fork Bull River, with locations of sampling reaches. The lower right inset map is the location of the study relative to the state of Montana. Maps were created using QGIS 3.4.7, with layers from the USGS National Hydrography Dataset.

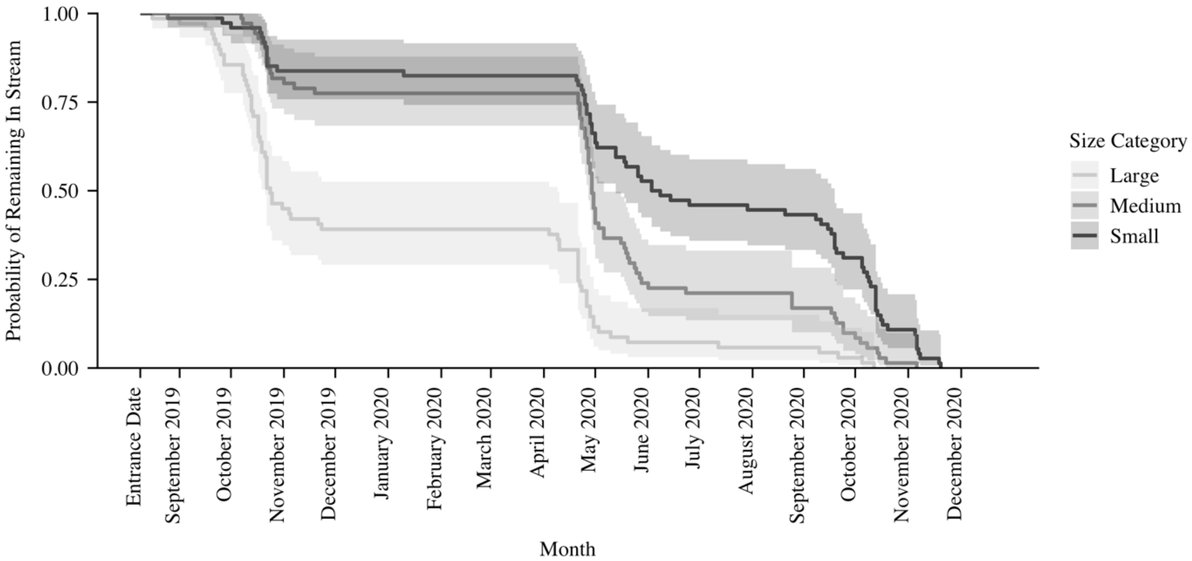

Figure 3.2. Probability of remaining in Graves Creek, Montana, for juvenile bull trout from the 2018 year-class, with grey scale delineating three size categories based on the length at time of summer electrofishing, small (n=74), medium (n=70), and large (n=70), and associated 95% confidence interval in grey.

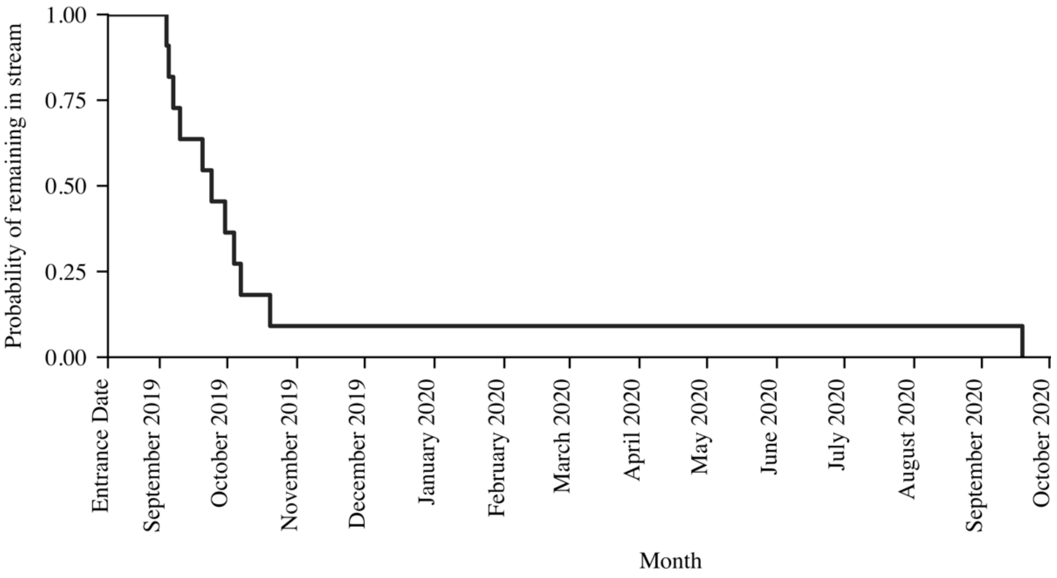

Figure 3.3. Probability of remaining in Graves Creek, Montana, for juvenile bull trout from the 2017 year-class initially encountered at age 2 (n = 30).

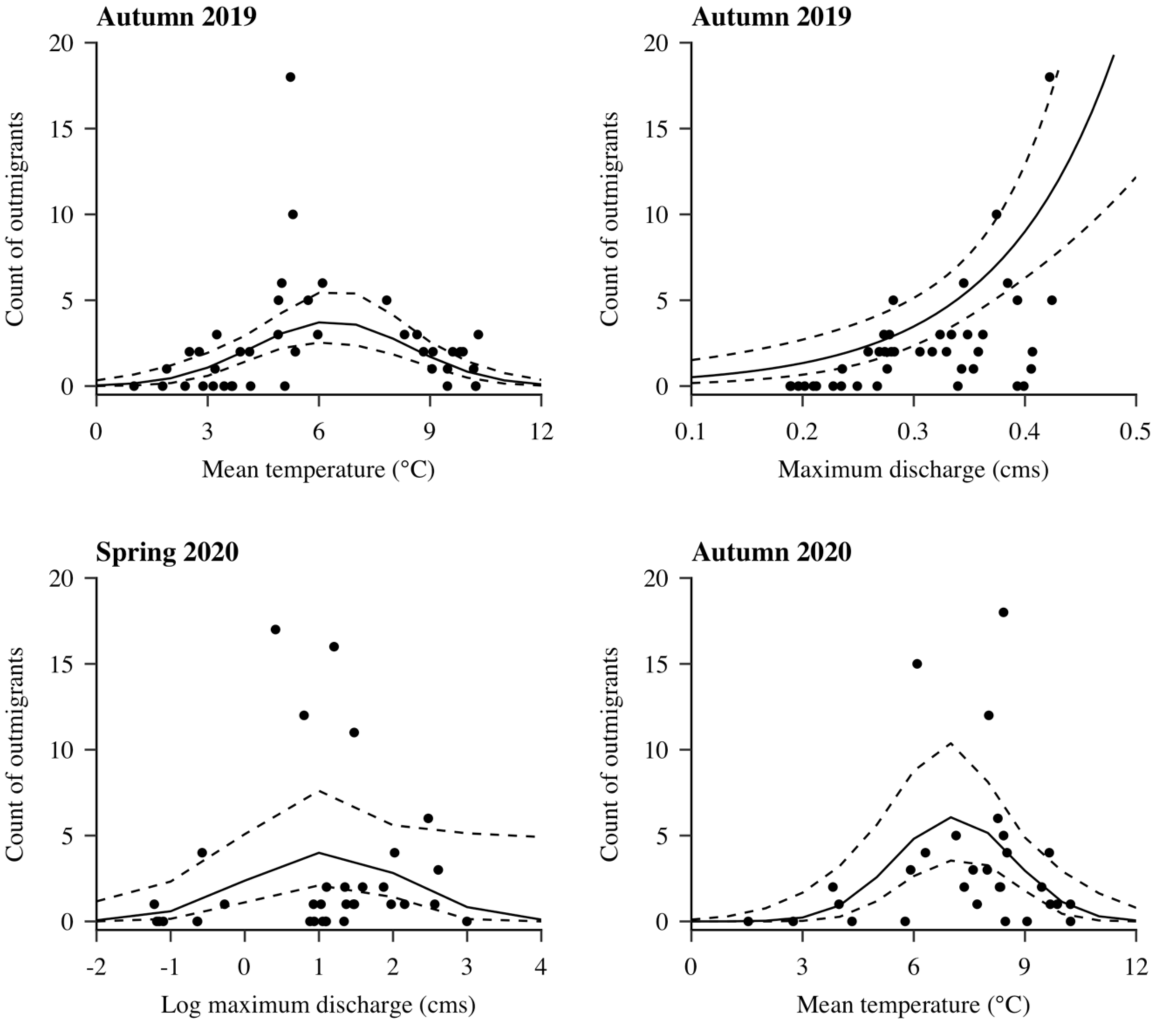

Figure 3.4. Relationship between abiotic factors and juvenile bull trout out-migration from Graves Creek, Montana, for top negative binomial GLM models. Solid lines delineate the predicted values from each model, with dotted lines representing 95% C.I., and points representing the observed counts of out-migrating bull trout. When more than one variable was present in the model, the variable not shown was held at its mean value.

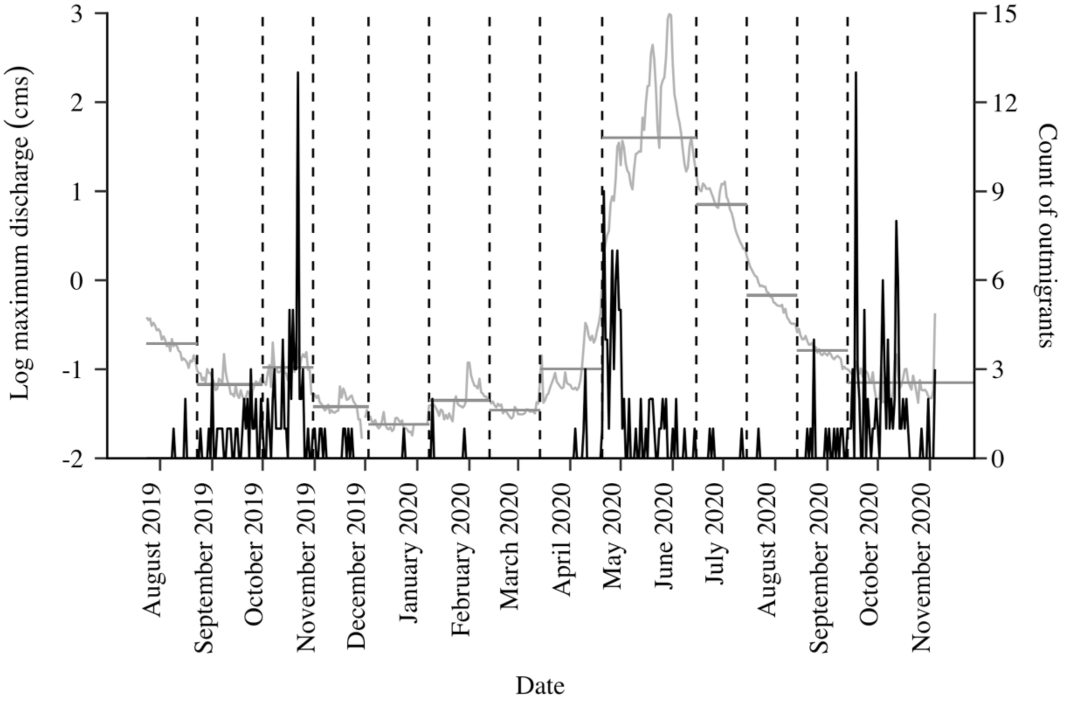

Figure 3.5. Time series from Graves Creek, Montana, from 25 July 2019 through 5 November 2020, with grey lines delineating time series of natural log-maximum daily discharge (cubic meters per second; cms) and black lines delineating time series of bull trout out-migrating by day. Dotted lines delineate changepoints, and horizontal lines represent the mean for each segment between changepoints.

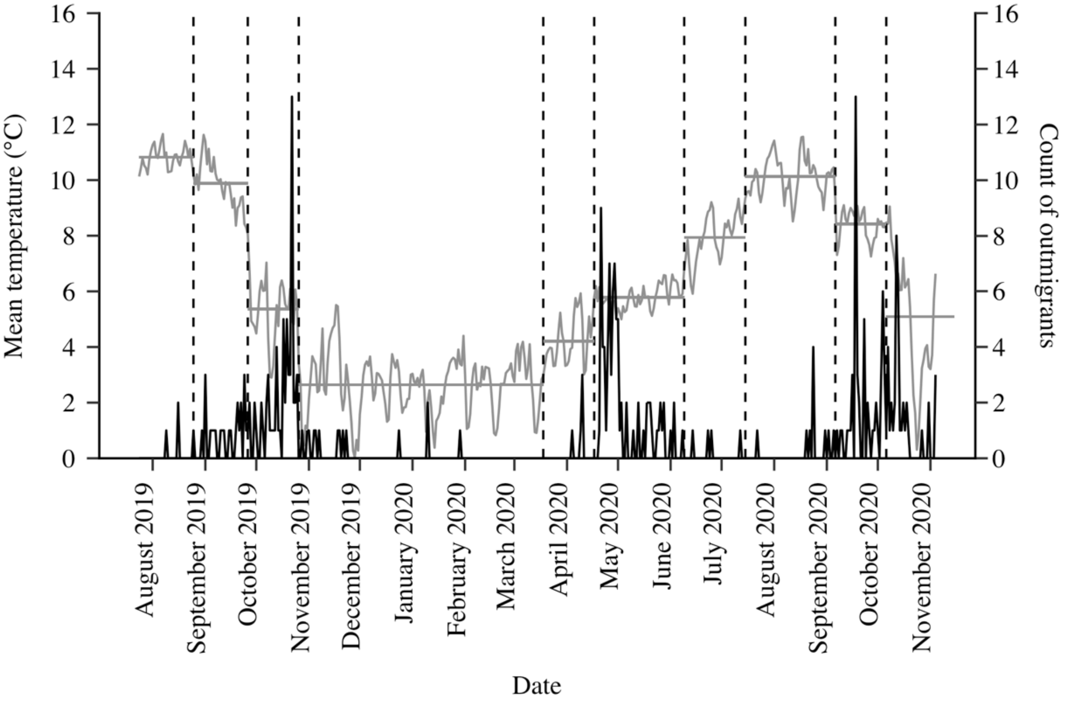

Figure 3.6. Time series from Graves Creek, Montana, from 25 July 2019 through 5 November 2020, with grey line delineating time series of mean daily water temperature (°C) and the black line delineating time series of bull trout out-migrating by day. Dotted lines delineate changepoints, and horizontal lines represent the mean for each segment between changepoints.

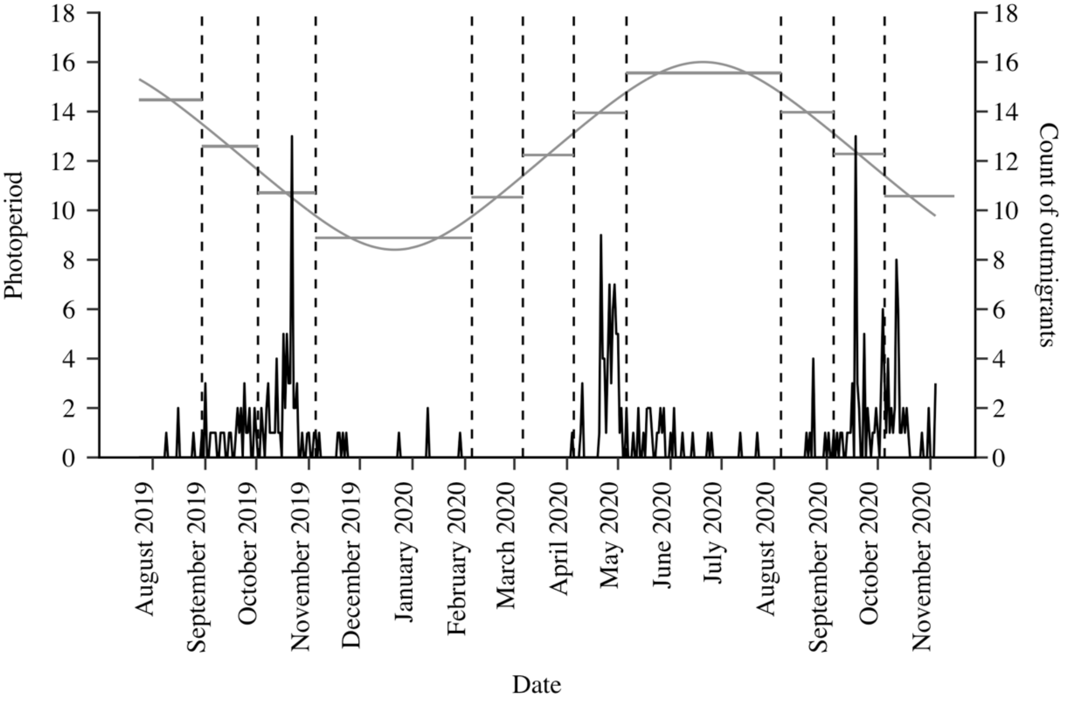

Figure 3.7. Time series from Graves Creek, Montana, from 25 July 2019 through 5 November 2020, with grey lines delineating time series of photoperiod and black lines delineating time series of bull trout out-migrating by day. Dotted lines delineate changepoints, and horizontal lines represent the mean for each segment between changepoints.

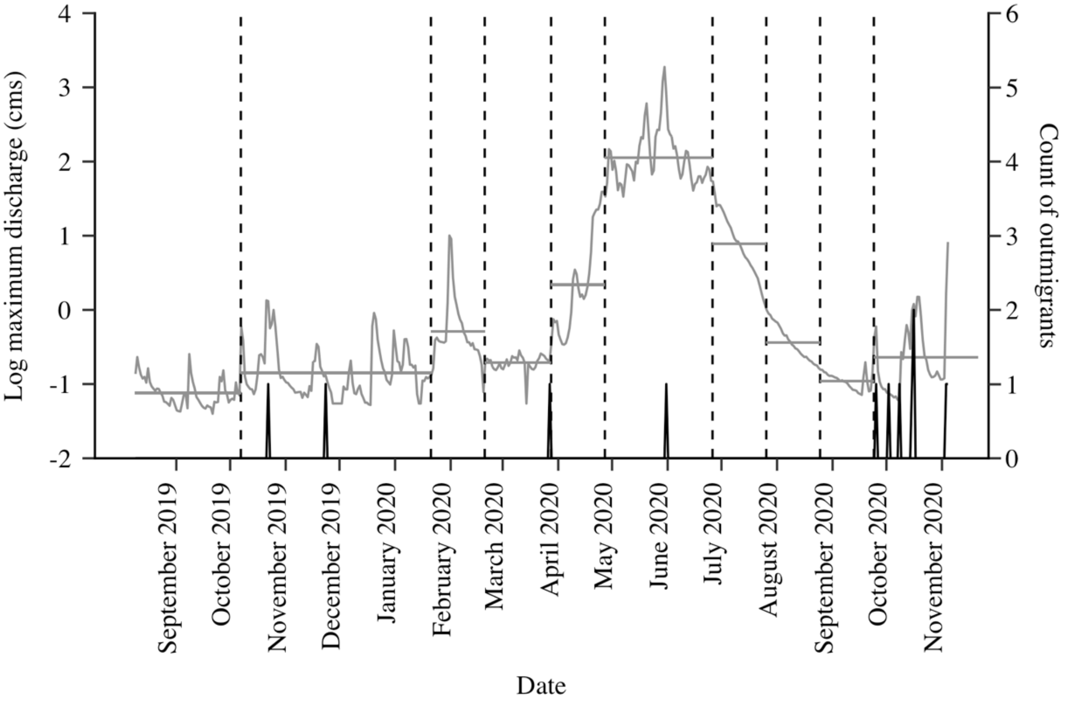

Figure 3.8. Time series from the East Fork Bull River, Montana, from 10 August 2019 through 5 November 2020, with grey lines delineating time series of natural log-maximum daily discharge (cubic meter per second; cms) and black lines delineating time series of bull trout out-migrating by day. Dotted lines delineate changepoints, and horizontal lines represent the mean for each segment between changepoints.

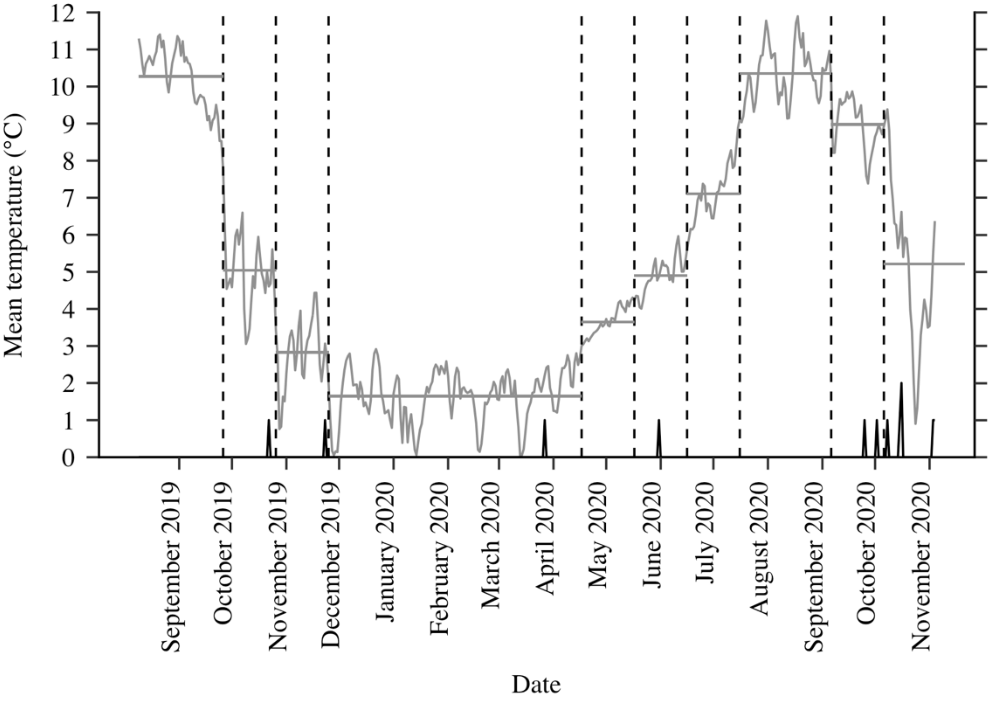

Figure 3.9. Time series from the East Fork Bull River, Montana, from 10 August 2019 through 5 November 2020, with grey lines delineating time series of mean daily water (°C) and black lines delineating time series of bull trout out-migrating by day. Dotted lines delineate changepoints, and horizontal lines represent the mean for each segment between changepoints.

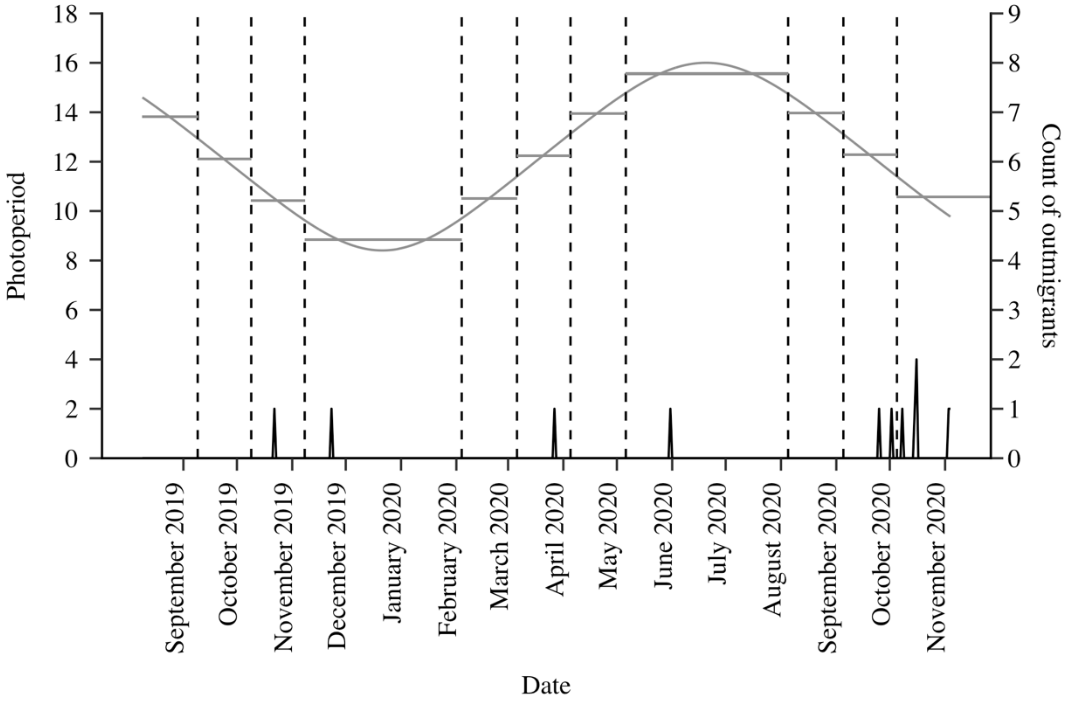

Figure 3.10. Time series from the East Fork Bull River, Montana, from 10 August 2019 through 5 November 2020, with grey lines delineating time series of photoperiod and black lines delineating time series of bull trout out-migrating by day. Dotted lines delineate changepoints, and horizontal lines represent the mean for each segment between changepoints.

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APPENDICES

APPENDIX A

RELATIVE CONDITION FACTOR OF JUVENILE BULL TROUT IN GRAVES CREEK AND EAST FORK BULL RIVER

Relative condition factor (K_n) was calculated in Graves Creek and East Fork Bull River in the summer of 2019 and 2020 with the following formula (Neumann et al. 2012):

$$K_n = \frac{W}{W'},$$

where W is the weight of an individual Bull Trout, and W′ is the predicted weight of an individual Bull Trout, based on a regression fit to $\log_{10}$ transformed weight and length data from the population (Neumann et al. 2012). Plots and regression equations are shown below.

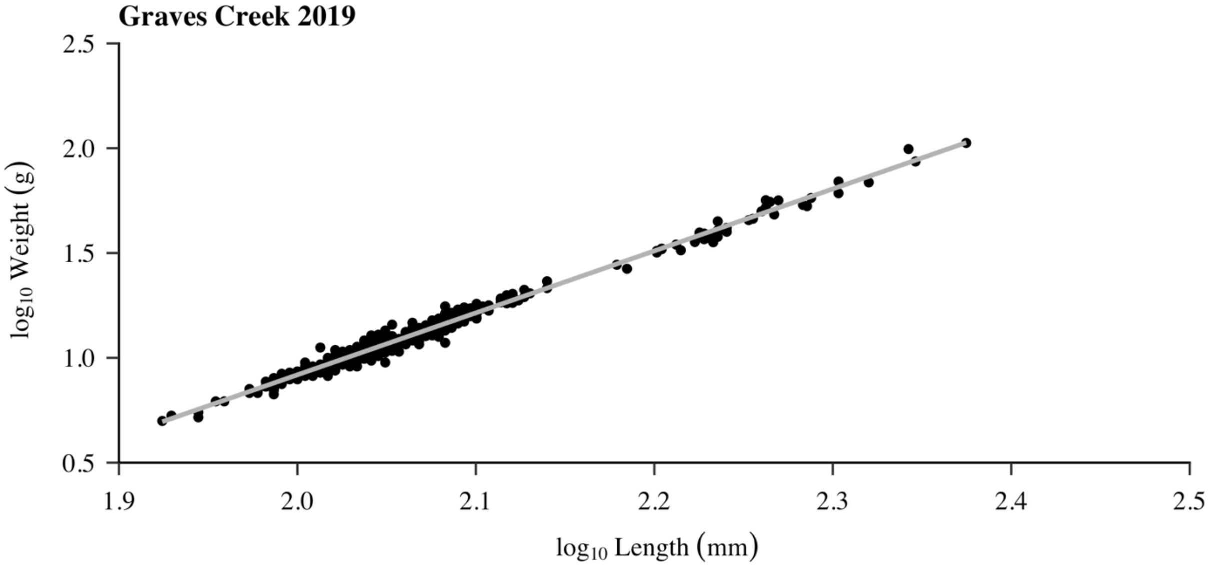

Figure A.1. Plot of $\log_{10}$ transformed total length (mm) and weight (g) from Graves Creek, regression equation: $\log_{10}(W') = -4.993 + 2.956(\log_{10} \text{Length})$.

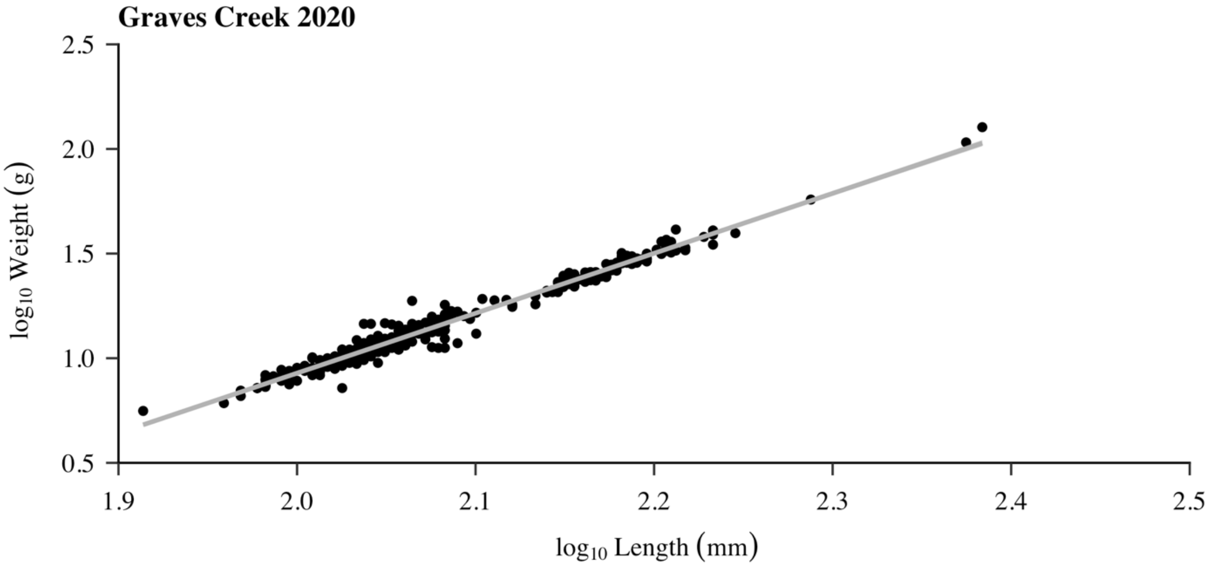

Figure A.2. Plot of $\log_{10}$ transformed total length (mm) and weight (g) from Graves Creek, regression equation: $\log_{10}(W') = -4.798 + 2.863(\log_{10}\text{Length})$.

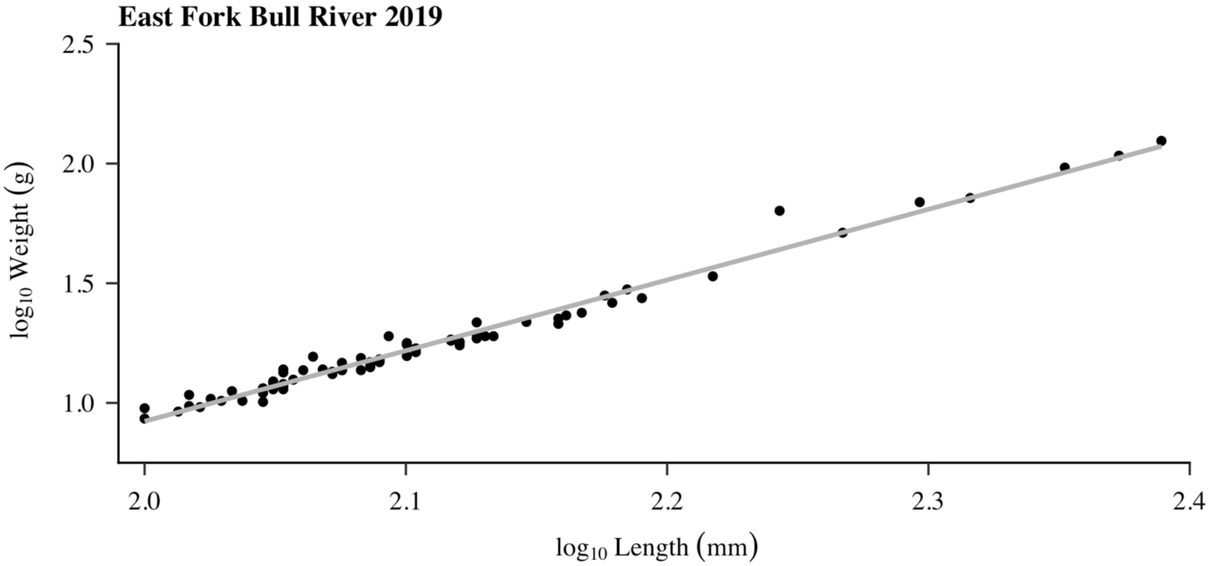

Figure A.3. Plot of $\log_{10}$ transformed total length (mm) and weight (g) from East Fork Bull River, regression equation: $\log_{10}(W') = -5.043 + 2.981(\log_{10}\text{Length})$.

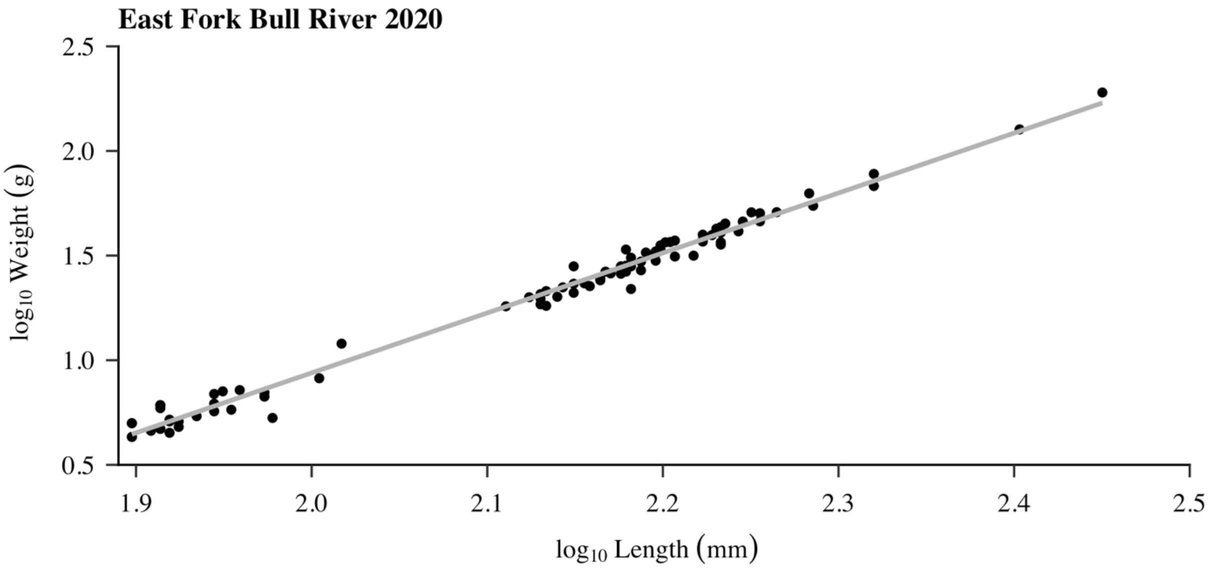

Figure A.4. Plot of $\log_{10}$ transformed total length (mm) and weight (g) from East Fork Bull River, regression equation: $\log_{10}(W') = -4.785 + 2.863(\log_{10} \text{Length})$.

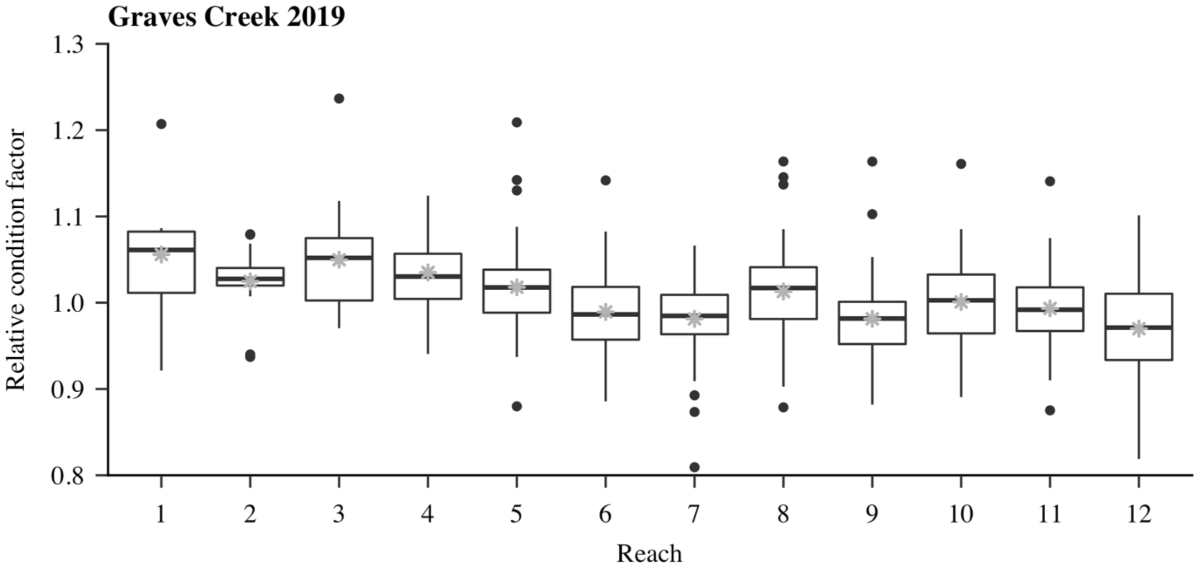

Figure A.5. Relative condition factor (K_n) by reach in Graves Creek 2019, with reaches labeled from downstream (1) to upstream (12), and grey star showing mean value.

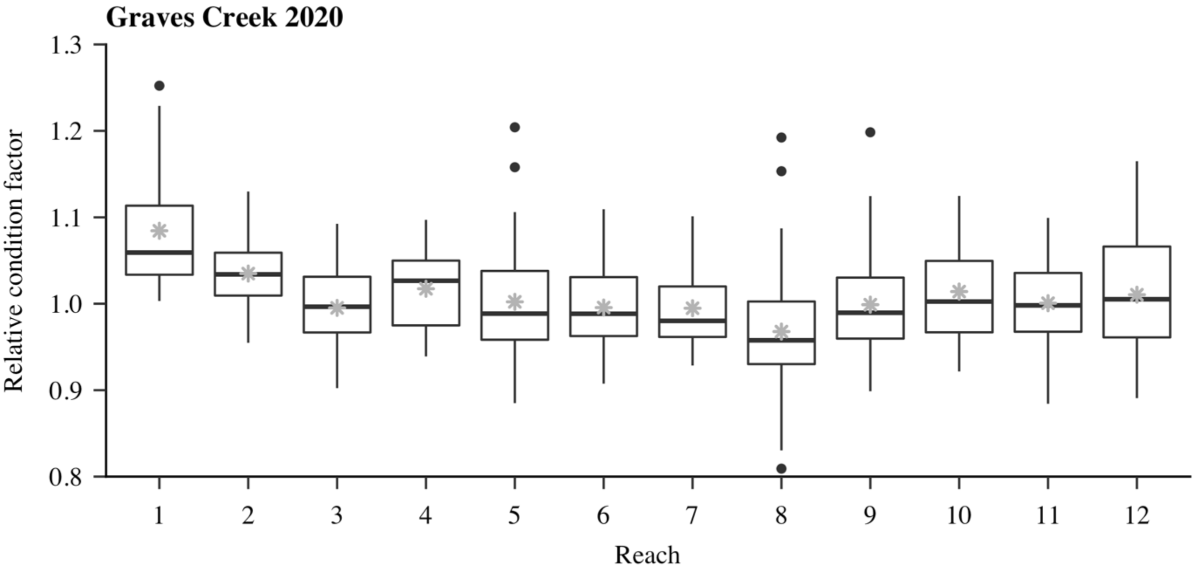

Figure A.6. Relative condition factor (K_n) by reach in Graves Creek 2020, with reaches labeled from downstream (1) to upstream (12), and grey star showing mean value.

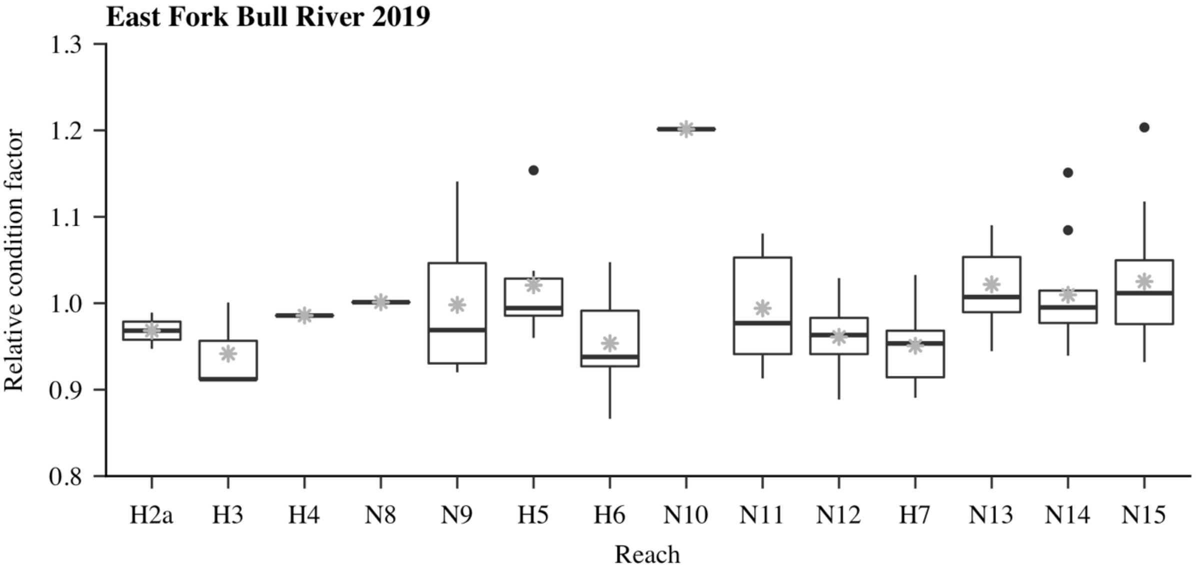

Figure A.7. Relative condition factor (K_n) by reach in East Fork Bull River 2020, with grey star showing mean value. Reaches are labeled from downstream (H3) to upstream (N15), with 'H' denoting historic electrofishing reaches and 'N' denoting new electrofishing reaches (H1a did not have any Bull Trout present.

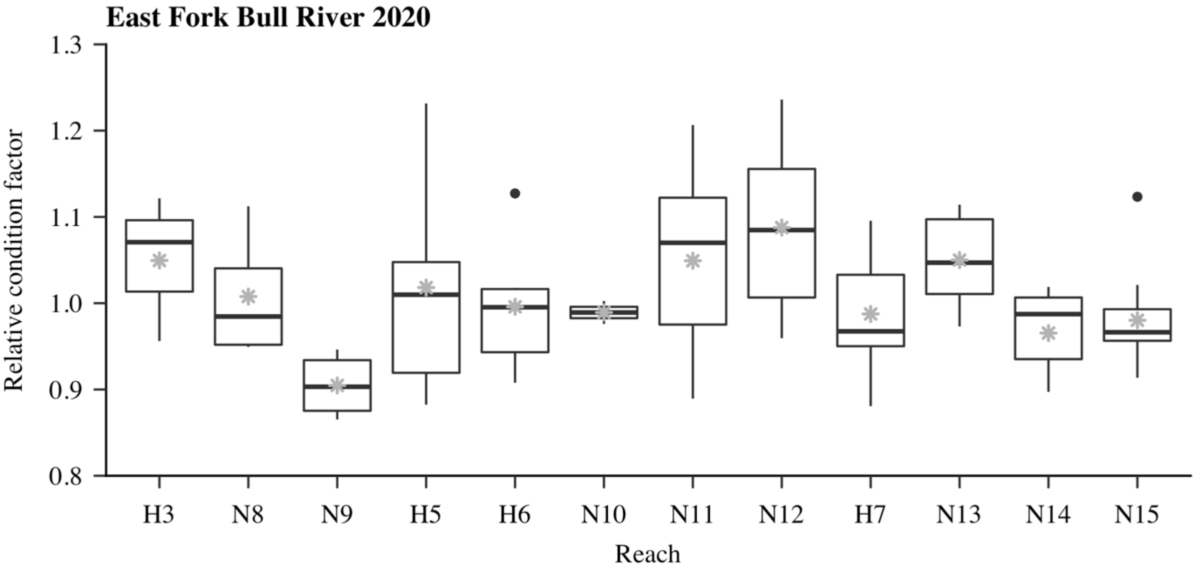

Figure A.8. Relative condition factor (K_n) by reach in East Fork Bull River 2020, with grey star showing mean value. Reaches are labeled from downstream (H3) to upstream (N15), with 'H' denoting historic electrofishing reaches and 'N' denoting new electrofishing reaches (H1a and H2a did not have any Bull Trout present).

APPENDIX B

AGE-LENGTH KEYS FOR GRAVES CREEK AND EAST FORK BULL RIVER

Table B.1. Probability of age given total length (mm) category in Graves Creek summer 2019.

Length Category	Probability of age		
	Age 1	Age 2	Age 3
80 - 89	1	0	0
90 - 99	1	0	0
100 - 109	1	0	0
110 - 119	1	0	0
120 - 129	1	0	0
130 - 139	1	0	0
140 - 149	0	1	0
150 - 159	0	1	0
160 - 169	0	1	0
180 - 189	0	1	0
190 - 199	0	1	0
200 - 209	0	0.67	0.33
220 - 229	0	0	1
230 - 239	0	0	1

Table B.2. Probability of age given total length (mm) category in Graves Creek summer 2020.

Length Category	Probability of age		
	Age 1	Age 2	Age 3
80 - 89	1	0	0
90 - 99	1	0	0
100 - 109	1	0	0
110 - 119	1	0	0
120 - 129	0.94	0.05	0
130 - 139	0	1	0
140 - 149	0	1	0
150 - 159	0	1	0
160 - 169	0	1	0
170 - 179	0	1	0
190 - 199	0	0	1
230 - 239	0	0	1
240 - 249	0	0	1

Table B.3. Probability of age given total length (mm) category in East Fork Bull River summer 2019.

Length	Probability of age			
Category	Age 1	Age 2	Age 3	Age 4+
100 - 109	1	0	0	0
110 - 119	0.56	0.44	0	0
120 - 129	0.11	0.89	0	0
130 - 139	0	1	0	0
140 - 149	0	0.5	0.5	0
150 - 159	0	0	1	0
160 - 169	0	0	1	0
170 - 179	0	0	1	0
190 - 199	0	0	1	0
200 - 209	0	0	0	1
220 - 229	0	0	0	1
230 - 239	0	0	0	1
240 - 249	0	0	0	1
330 - 339	0	0	0	1

Table B.4. Probability of age given total length (mm) category in East Fork Bull River summer 2020.

Length	Probability of age			
Category	Age 1	Age 2	Age 3	Age 4+
70 - 79	1	0	0	0
80 - 89	1	0	0	0
90 - 99	1	0	0	0
100 - 109	1	0	0	0
120 - 129	0	1	0	0
130 - 139	0	1	0	0
140 - 149	0	0.88	0.13	0
150 - 159	0	0	1	0
160 - 169	0	0	1	0
170 - 179	0	0	1	0
180 - 189	0	0	1	0
190 - 199	0	0	1	0
200 - 209	0	0	0	1
280 - 289	0	0	0	1

Table B.5. Probability of age given total length (mm) category in Graves Creek autumn 2019.

Length	Probability of age		
Category	Age 1	Age 2	Age 3
110 - 119	1	0	0
120 - 129	1	0	0
130 - 139	1	0	0
140 - 149	1	0	0
150 - 159	0.5	0.5	0
160 - 169	0	1	0
170 - 179	0	1	0
180 - 189	0	1	0
190 - 199	0	1	0
200 - 209	0	1	0
210 - 219	0	1	0
230 - 239	0	0	1

Table B.6. Probability of age given total length (mm) category in Graves Creek autumn 2020.

Length	Probability of age		
Category	Age 1	Age 2	Age 3
110 - 119	1	0	0
120 - 129	1	0	0
130 - 139	0.17	0.83	0
140 - 149	0	1	0
150 - 159	0	1	0
160 - 169	0	1	0
170 - 179	0	1	0
180 - 189	0	1	0
190 - 199	0	0	1

APPENDIX C

ESTIMATED TOTAL ABUNDANCE OF BULL TROUT IN GRAVES CREEK AND EAST FORK BULL RIVER

To estimate the total abundance of Bull Trout in Graves Creek and East Fork Bull River, the approximate river kilometers of the downstream and upstream ends of the reaches were determined using the ‘riverdist’ package in R (Tyers 2016). Using the approximate river kilometers, the distance between reaches was estimated, and multiplied by the mean abundance per meter of Bull Trout in reaches directly above and below the area (e.g., the approximate distance between the top of reach 1 and the bottom of reach 2 would be multiplied by the mean Bull Trout per meter of reach 1 and 2). The procedure was repeated using the high and low abundance estimates. The abundance estimates for Graves Creek and East Fork Bull River were limited to the area between the bottom of reach 1 and the top the upstream most reach to avoid extrapolating.

Table C.1. Total population abundance estimates from Graves Creek and East Fork Bull River in summer 2019 and 2020, with low and high estimates from 95% prediction intervals.

Year	Total Population Abundance	Low Estimate	High Estimate
Graves Creek			
2019	2082	1793	2371
2020	1556	1277	1836
East Fork Bull River			
2019	547	318	775
2020	640	462	818

Reference

Matt Tyers (2020). riverdist: River Network Distance Computation and Applications. R package version 0.15.3. https://CRAN.R-project.org/package=riverdist

APPENDIX D

SPATIAL DISTRIBUTION OF JUVENILE BULL TROUT BY AGE IN GRAVES CREEK AND EAST FORK BULL RIVER

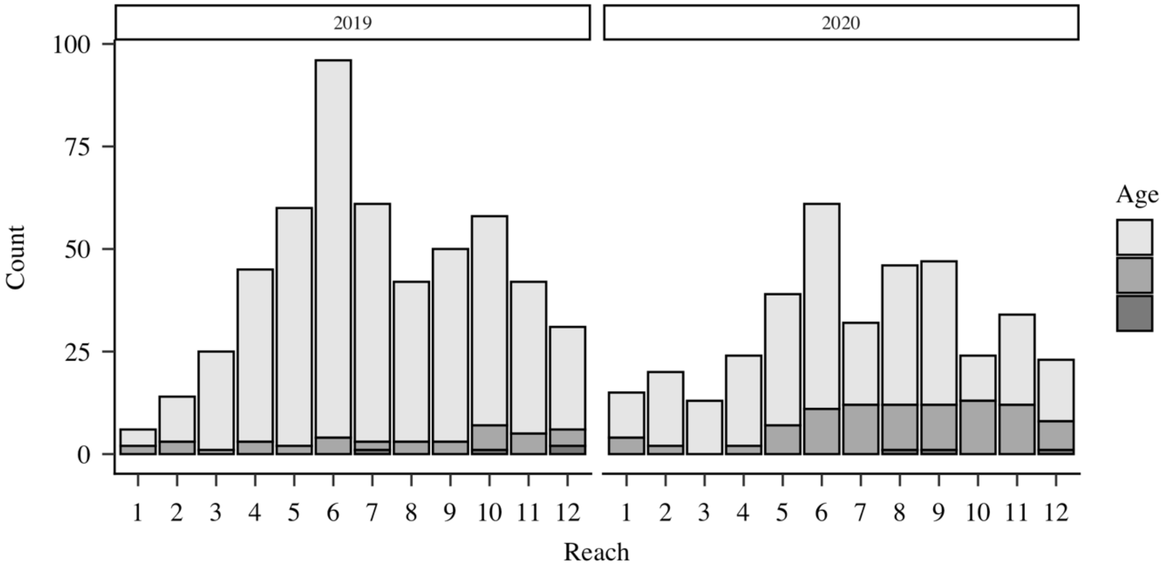

Figure D.1. Number of sampled Bull Trout in Graves Creek by reach (from downstream most to upstream) with grey scale denoting age.

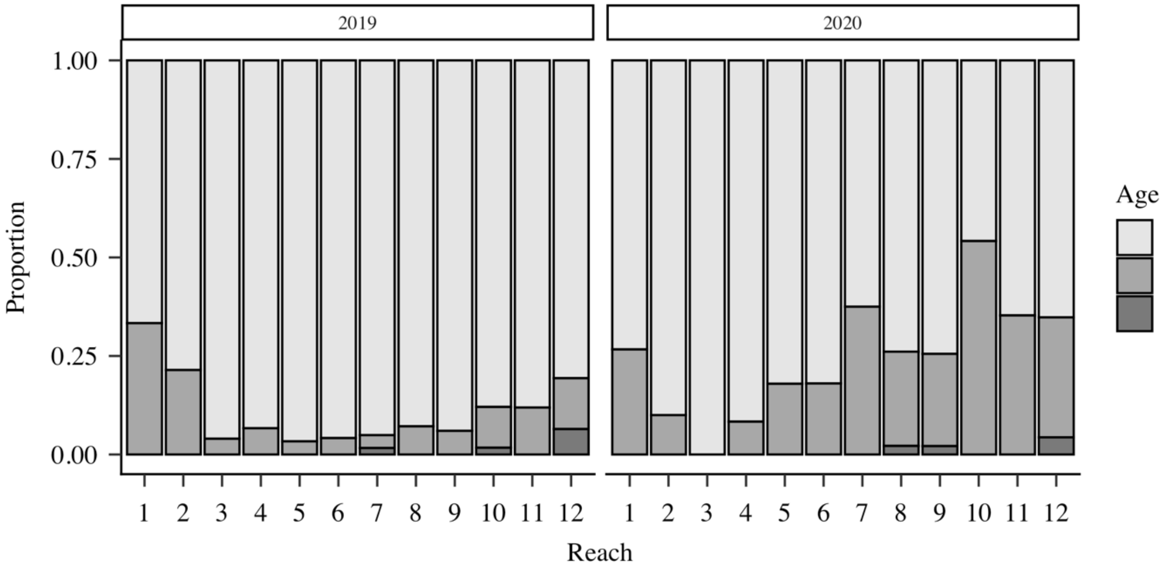

Figure D.2. Proportion of age-class present in each reach in Graves Creek with grey scale denoting age.

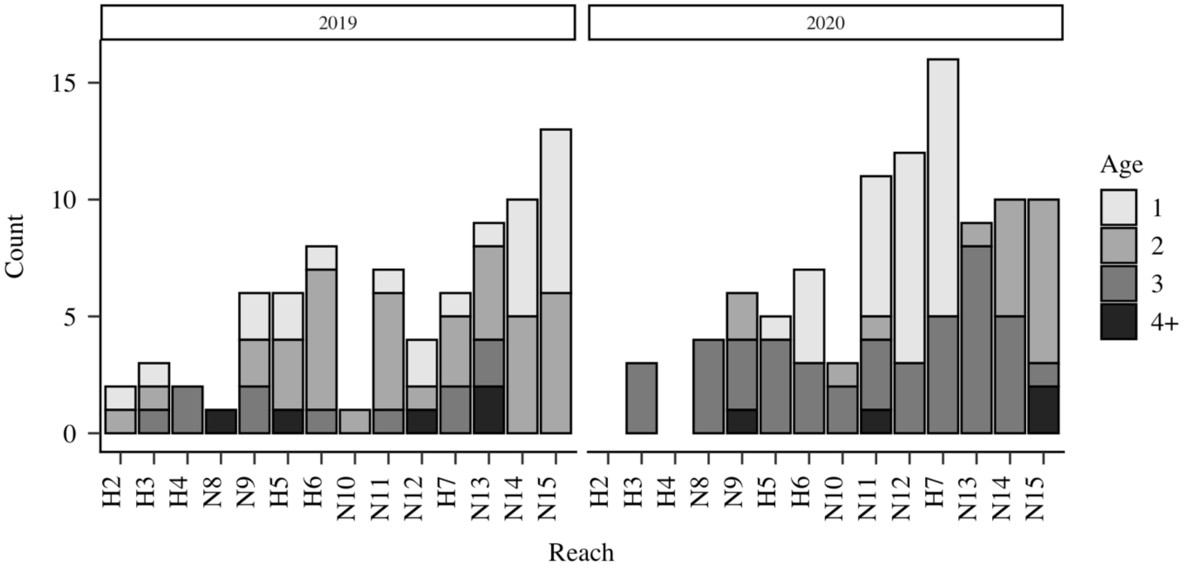

Figure D.3. Number of sampled Bull Trout in East Fork Bull River by reach (from downstream most to upstream) with grey scale denoting age.

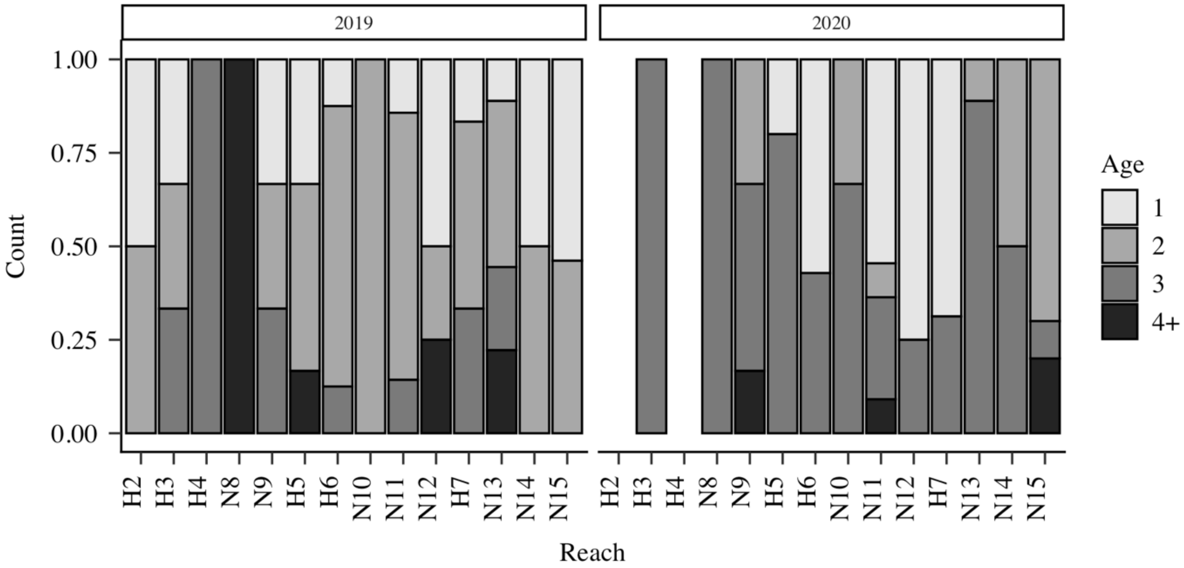

Figure D.4. Proportion of age-class present in each reach in East Fork Bull River with grey scale denoting age.

APPENDIX E

CONDITION SPECIFIC TRAP EFFICIENCY OF PERMANENT WEIR IN GRAVES CREEK

Table E.1. Monthly capture efficiency of the permanent weir in Graves Creek, calculated as the proportion of the number of tagged, out-migrating bull trout that were captured, over the total number of tagged out-migrating Bull Trout (captured or missed). Bull trout that out-migrated when the trap was set for volitional passage, or not fishing for a weekend or holiday were not considered. Maximum discharge (cms) is summarized for when fish were missed by the trap, and when fish were captured, and the columns show the mean maximum discharge and the range of maximum discharge. Proportion of missed Bull Trout that were age 1 and age 2 is shown (no age-3 bull trout were missed during trapping seasons).

Month and year	Tagged out-migrants (n)	Capture efficiency (%)	Maximum discharge (cms) when fish are missed (mean [min – max])	Maximum discharge (cms) when fish are captured (mean [min – max])	Proportion of age-1 missed (n)	Proportion of age-2 missed (n)
September 2019	19	84.2	0.30 (0.29-0.32)	0.29 (0.25-0.33)	0.7 (2)	0.3 (1)
October 2019	59	91.5	0.44 (0.37-0.50)	0.39 (0.32-0.50)	1.0 (5)	0.0 (0)
November 2019	9	55.6	0.28 (0.26-0.28)	0.26 (0.23-0.30)	1.0 (4)	0.0 (0)
April 2020	38	21.1	2.68 (1.36-4.48)	1.77 (0.98-2.57)	-	1.0 (30)
May 2020	22	0	7.90 (3.32-14.07)	-	-	1.0 (22)
June 2020	6	16.7	4.90 (2.54-7.28)	2.81 (2.81-2.81)	-	1.0 (5)
September 2020	29	100	-	0.32 (0.24-0.44)	0.0 (0)	0.0 (0)
October 2020	46	100	-	0.37 (0.30-0.45)	0.0 (0)	0.0 (0)
November 2020	18	83.3	0.55 (0.55-0.55)	0.52 (0.27-0.69)	0.0 (0)	1.0 (3)

APPENDIX F

RECOMMENDATIONS FOR FUTURE RESEARCH AND MANAGEMENT IMPLICATIONS

East Fork Bull River

- Continued monitoring of Bull Trout tagged during this study will be necessary to fully understand the out-migration dynamics of juvenile Bull Trout in East Fork Bull River. In Graves Creek, 37.5% of tagged Bull Trout were detected out-migrating over the course of the study, whereas in East Fork Bull River, 12.5% of tagged Bull Trout were detected out-migrating. Given that Bull Trout in Graves Creek out-migrated primarily at age 1 and age 2, with few remaining to reach age 3, the duration of this study likely captured the majority of out-migration that occurred from the 2017 and 2018 year-class of Bull Trout in Graves Creek. In East Fork Bull River, Bull Trout out-migrated at age 2, age 3, and age 4. As a result, the duration of this study likely did not capture the full extent of out-migration from any of the year-classes tagged in East Fork Bull River. Monitoring for the next two years will allow for a better understanding of out-migration dynamics in East Fork Bull River by quantifying what proportion of the 2017 year-class will out-migrate at age 4 and age 5, and the proportion of the 2018 year-class that will out-migrate at age 3 and age 4. Due to the reduced size of Bull Trout in the 2019 year-class, only 2 of the 31 Bull Trout could be tagged, therefore inferences regarding out-migration at age 1 is limited to knowledge from the 2018 year-class. Although continued monitoring will likely increase the proportion of fish tagged during this study that are detected out-migrating, the proportion will likely remain below Graves Creek due to natural mortality. With a longer time between tagging and out-migration as a result of an older age at out-migration, Bull Trout tagged in the East Fork Bull River are more vulnerable to natural in-stream mortality before out-migrating when compared to Graves Creek.

- Improve capture efficiencies of traps. Capture efficiency in East Fork Bull River was very low, of the 18 tagged Bull Trout out-migrating from East Fork Bull River, only one was captured in a trap. Low capture efficiencies mean that the number of Bull Trout captured in the trap likely do not reflect the magnitude of out-migration from East Fork Bull River. With the older age at-out-migration in East Fork Bull River when compared to Graves Creek, we would generally expect lower numbers of out-migrating Bull Trout; however, these fish are expected to have a greater chance of surviving to reach maturity. Therefore, it is imperative that efforts are made to increase the efficiency of the current trapping efforts, which may require the construction of a permanent structure similar to the weir trap on Graves Creek.

Graves Creek

- Consistently sample and tag Bull Trout in Graves Creek during summer months. Continuing to sample and tag Bull Trout in Graves Creek will be necessary to allow for continued monitoring of the population abundance, out-migration dynamics, and capture efficiency of the permanent weir. As Graves Creek approaches carrying capacity, monitoring of population abundance will be necessary to understand the stock-recruitment dynamics of the population, which may potentially enable Bull Trout to be translocated from Graves Creek to other tributaries. Sampling efforts should be standardized to facilitate comparison among years. Tagging fish during the summer will also allow for out-migration timing to be monitored temporally to ensure that trapping seasons continue to capture the majority of out-migration, and do not begin to select for or against early or late out-migrating fish.

- Quantify capture efficiency on a consistent basis. Understanding capture efficiency is necessary to quantify the total out-migration of bull trout, and to understand the overall efficacy of the trapping efforts to capture fish of varying sizes, ages, and during varying abiotic conditions. Use of tagged fish as described in this study can provide capture efficiency estimates, however, this would require that an adequate number of Bull Trout are tagged prior to out-migration. Trial-and-error will be necessary to determine the amount of sampling effort needed to ensure that the sample size of tagged fish out-migrating is large enough to make statically rigorous conclusions. If the number of tagged fish is low, conducting capture efficiency trials by re-releasing fish upstream of the traps may be necessary to continue to quantify capture efficiency. Although there are drawbacks to this method, it does allow for the control of sample size at varying conditions and could be implemented in conjunction with the use of tagged fish.
- Remove and age scales from Bull Trout during summer sampling and during trapping seasons. Understanding the age structure of the populations is necessary to develop accurate stock-recruitment relationships, and age-at-out-migration has implications for survival of out-migrating Bull Trout. We found significant variation in length-at-age between tributaries and within tributaries between years, indicating that length used as a surrogate for age may be inaccurate among years. Continuing to remove and age scales from a subset of Bull Trout in each size category is necessary to ensure that the correct age is being assigned to fish.
- Quantify condition specific detection probability of stationary PIT-antennas. Detection probability of the stationary PIT-antennas can vary based on conditions, and this

variation can potentially bias the understanding of out-migration dynamics of Bull Trout. In particular, high flows during the spring trapping seasons may reduce detection probability, which would lead to an underestimation of spring out-migration. If detection probability can be quantified, estimates can be adjusted as needed to account for the lowered probability.

APPENDIX G

MEAN DAILY WATER TEMPERATURE IN GRAVES CREEK AND EAST FORK BULL RIVER

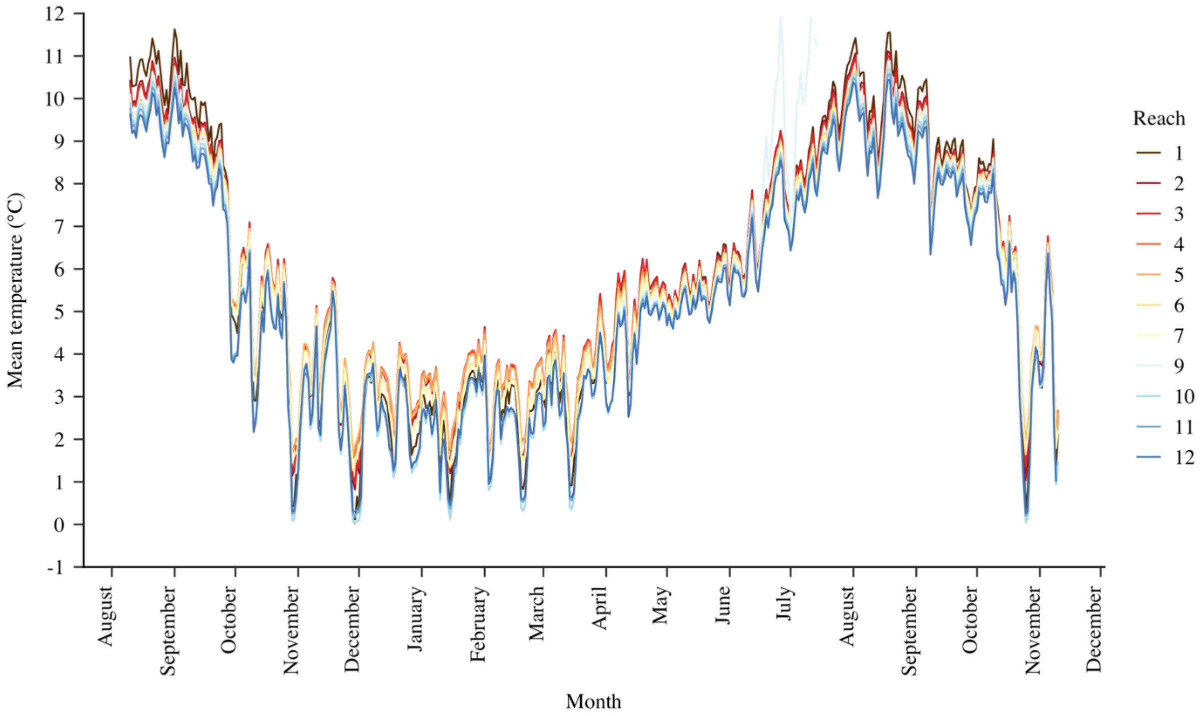

Figure G.1. Mean daily water temperature in Graves Creek with colors representing reaches. The temperature logger in reach 8 was not recovered, and the temperature logger in reach 9 was out of the water from June 2020 – August 2020.

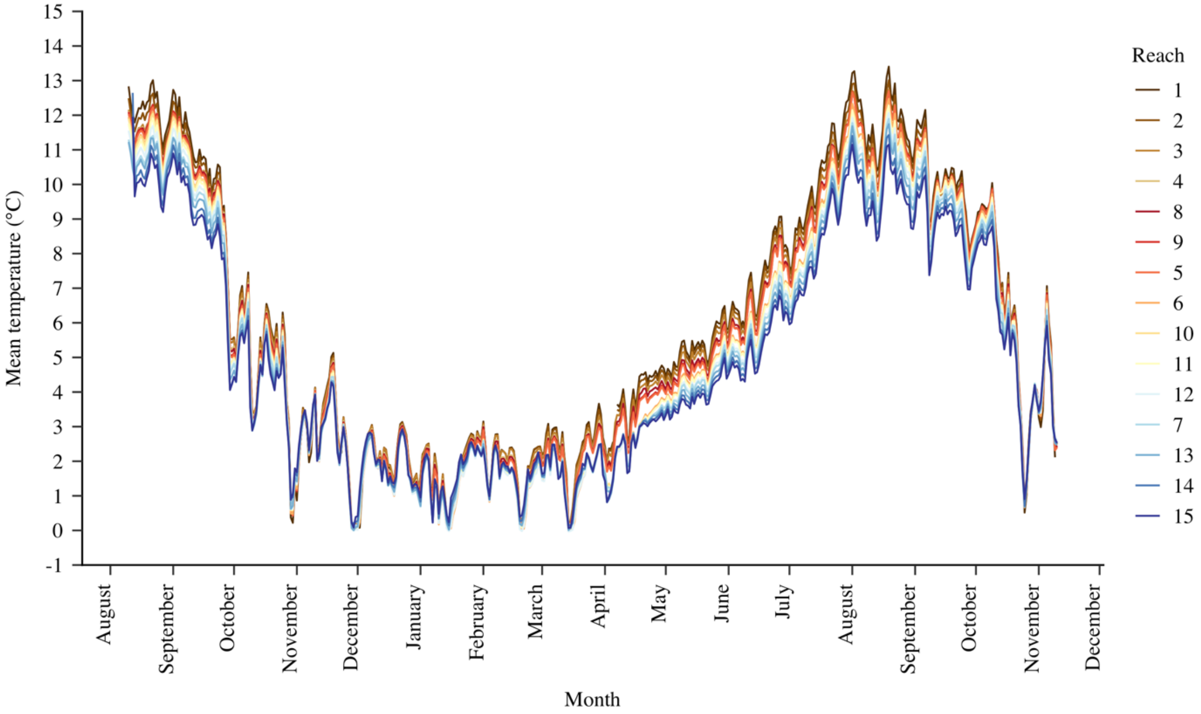

Figure G.2. Mean daily water temperature in East Fork Bull River with colors representing reaches. The temperature logger in reach 4 came loose from the cable between August 2020 and November 2020 and was located in December about 60 m downstream. The temperature loggers in reaches 5 and 9 were out of the water when checked in August 2020 and were placed back into the water. The temperature logger in reach 10 was suspected to have been out of the water during low flows.