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Population and outmigration characteristics of juvenile Bull Trout in a montane ecosystem

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Abstract

Bull Trout *Salvelinus confluentus* is a federally threatened species in the conterminous United States. Although some populations are stable or increasing, Bull Trout in the United States Fish and Wildlife Service's designated Coeur d'Alene Core Area in Idaho have experienced substantial declines in abundance. Today, the remaining extant population in the Coeur d'Alene Core Area returns to the headwaters of the St. Joe River to spawn. The population has been monitored annually since 1992 using spawning ground surveys, but little is known about early life stages in the system. The objective of our research was to evaluate the distribution and abundance, age and size structure, habitat associations, and outmigration characteristics of juvenile Bull Trout in the upper St. Joe River basin. In 2022–2023, we sampled 200 stream reaches on the mainstem St. Joe River and four tributaries (Heller, Medicine, Sherlock, and Wisdom creeks). We sampled 1,529 Bull Trout varying in length from 29–257 mm in total length (TL; mean ± SD; 108 ± 44 mm). Population estimates suggested there were 1,841 (95% CI = 1,188–2,494) juvenile Bull Trout in the study area in 2022 and 2,388 (1,646–3,130) in 2023. Regression models indicated that abundance was positively related to canopy cover, amount of large substrate, amount of large woody debris, and amount of gravel, and negatively related to water temperature. We tagged 1,142 fish with passive integrated transponders (PIT) and detected 163 (14%) of these fish using a stationary tag array that was operational during June or July through October. Peak autumn outmigration occurred in October of both sampling years. Of the

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fish that were detected moving, age varied from 1–4 years, but age-1 and age-2 fish were more commonly detected moving downstream compared to other age classes. This study provides important information on the ecology of juvenile Bull Trout that can be used to guide conservation and recovery efforts in montane ecosystems. Furthermore, juvenile Bull Trout in the upper St. Joe River basin were present at similar densities and experienced growth rates similar to more robust adfluvial populations (e.g., Lake Pend Oreille, Idaho), thereby indicating that factors contributing to the low abundance of adults are not likely occurring in the headwaters of the St. Joe River. Thus, conservation efforts may be more successful if they are focused on the migration corridor and Coeur d'Alene Lake.

KEYWORDS

age and growth, Bull Trout ecology, Endangered Species Act, habitat, montane ecosystems, outmigration

The disturbance of freshwater ecosystems and introduction of nonnative fish species in western North America have led to substantial declines in distribution and abundance of salmonid populations (Penaluna et al. 2016). Not only are salmonids sensitive to changes in physical habitat characteristics (e.g., sediment, temperature), but the life history of many salmonids often includes a migratory component that can be affected by impoundments (e.g., Caudill et al. 2013). Barriers to movement prevent salmonids from reaching spawning grounds and optimal rearing habitat (Behnke 1992). Native salmonids are also highly sensitive to interactions with nonnative species (Quist and Hubert 2004, Rahel et al. 2007, Voss et al. 2023). Given the sensitivities of salmonids to altered habitat and fish assemblages, most salmonid species native to western North America have experienced declines (Muhlfeld et al. 2019). In particular, Bull Trout *Salvelinus confluentus* populations have experienced substantial reductions in distribution and abundance.

Bull Trout is a char native to Idaho, Montana, Nevada, Oregon, Washington, and western Canada (U.S. Fish and Wildlife Service [USFWS] 2015). Bull Trout exhibit multiple life-history strategies, including adfluvial, fluvial, and resident, that are often present within and between populations (Rieman and McIntyre 1993). Additionally, some anadromy has been observed in coastal populations (Cavender 1978). Alternate life-history strategies likely increase resilience of populations to environmentally stochastic events, thereby increasing long-term population persistence (Rieman and McIntyre 1993, Rieman and Allendorf 2001, Hilborn et al. 2003).

Bull Trout is culturally and ecologically important throughout its native distribution (Issak et al. 2014). Historically, they were important to tribes of the Pacific Northwest that traditionally fished in waters not accessible to anadromous salmonids (Colombi 2012). Additionally, the relatively large size of adults and aggressive behavior make them a popular recreational species. Bull Trout was listed in 1999 as threatened in the contiguous United States under the U.S. Endangered Species Act because of declines in abundance throughout its native distribution (USFWS 1999). At the time of listing, they had been extirpated from approximately 60% of their historical distribution (Quigley and Arbelbide 1997). The USFWS drafted the first recovery plan for the species in 2002, which focused on conserving genetic diversity, maintaining life-history features, and ensuring broad geographical representation of populations (USFWS 2015). The recovery plan identifies six recovery units composed of smaller core areas in the coterminous United States. In 2008, an evaluation of the 121 core areas in the six recovery units indicated that 18 populations were stable, 14 were increasing, 23 were declining, and the status of 66 populations was unknown (USFWS 2015).

Populations are stable or increasing in most of the 35 core areas of the Columbia Headwaters Recovery Unit; however, the population in the Coeur d'Alene Lake Core Area (CDACA) is of particular concern.

All Bull Trout in the CDACA are thought to exhibit an iteroparous adfluvial life history. Historically, they were present throughout the St. Joe River and Coeur d'Alene River basins. However, because of land use disturbances and interactions with nonnative fish species, the only extant population in the CDACA spawns in the headwaters of the upper St. Joe River basin (USJRB; USFWS 2015). Annual spawning ground surveys conducted since 1992 by the Idaho Department of Fish and Game (IDFG) have indicated a decline in the abundance of Bull Trout redds in the USJRB, but causal factors are unknown (IDFG 2021). Results of those surveys indicated that redds were almost entirely limited to the index reaches. The mainstem St. Joe River and tributaries in the USJRB (i.e., Heller Creek, Medicine Creek, Sherlock Creek, Wisdom Creek) appear to provide quality habitat, but annual redd counts continue to decline (USFWS 2015).

The reduced distribution and low density of Bull Trout in the CDACA make the population exceptionally vulnerable to extirpation (USFWS 2015). However, factors limiting production in the USJRB are unknown. Addressing limiting factors requires a better understanding of juvenile population demographics in the system. The objective of this research was to provide a comprehensive understanding of juvenile Bull Trout ecology in the USJRB. Specifically, because of the limited knowledge about which tributaries are used by rearing juveniles in the basin and how many fish are present, we investigated juvenile distribution and abundance. A potential reason for low production could be that rearing habitat is limited in the headwater streams; therefore, we evaluated the relationship between abundance and habitat characteristics to provide insight into potential factors influencing juvenile Bull Trout in the study area. Another objective of this study was to evaluate the age and length structure of the population and to estimate growth of individuals. An understanding of when individuals are emigrating and immigrating is also important for making inferences about population rate functions and life-history strategies of a migratory population. Therefore, the last objective of this study was to investigate outmigration characteristics in the uppermost 16 km of the St. Joe River watershed.

STUDY AREA

The CDACA encompasses the Coeur d'Alene subbasin in the Columbia River basin. The Coeur d'Alene subbasin drains into Coeur d'Alene Lake, Idaho's second largest natural lake (12,700 ha). The two largest tributaries to Coeur d'Alene Lake are the St. Joe and Coeur d'Alene rivers, and the only outlet is the Spokane River. We sampled the mainstem of the upper St. Joe River and four tributaries (i.e., Heller, Medicine, Sherlock, Wisdom creeks) from June–August, 2022–2023 (Figure 1). All sampling occurred in the Wild and Scenic designated portion of the St. Joe River drainage in the Idaho Panhandle National Forest (Figure 1). The study area consisted of approximately 33 km of streams in the USJRB. The most downstream reaches in the study area were located approximately 233 km upstream from Coeur d'Alene Lake. Most streams included in the study were small (<3 m wetted width), including the mainstem St. Joe River, which is approximately 7–10 m wide. Surrounding forests are dominated by subalpine fir *Abies lasiocarpa* and lodgepole pine *Pinus contorta*. Stream channel elevation varies from 1,425 m to 1,694 m. Due to snowpack, the study area is only accessible in most years to 4×4 passenger vehicles from early July to late October. Native fishes in the study area include Bull Trout, Westslope Cutthroat Trout *Oncorhynchus lewisi*, Cedar Sculpin *Cottus schitsuumsh*, and Shorthead Sculpin *C. confuses*. Kokanee *O. nerka* is the only nonnative fish species in the USJRB.

METHODS

Fish and habitat sampling

Annual redd count surveys conducted by IDFG have indicated that recent spawning activity of Bull Trout is present in each tributary and the uppermost 16 km of the mainstem St. Joe River. Additionally, these are the largest

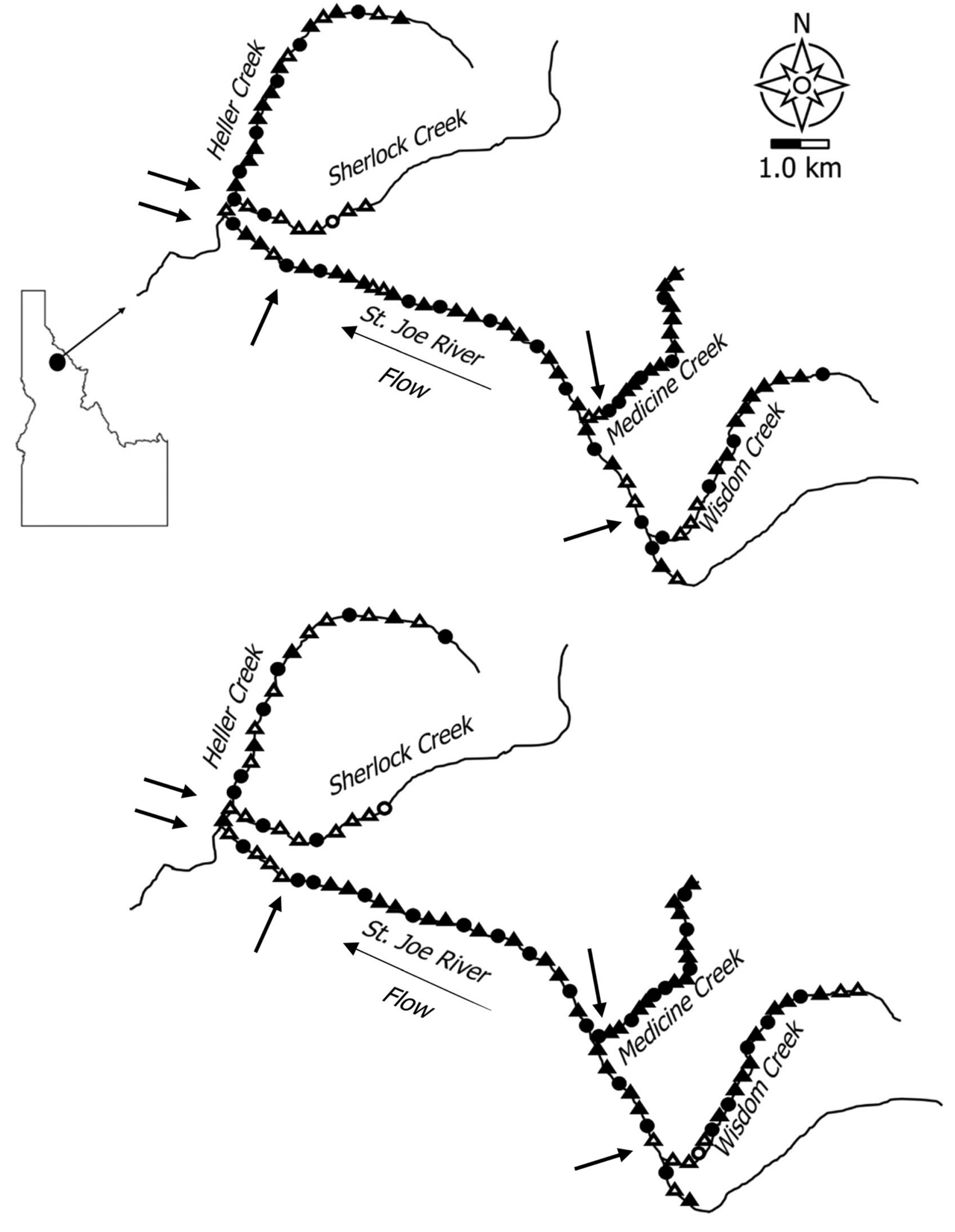

FIGURE 1 Sampling reaches where we conducted multiple-pass depletion (circle) and single-pass surveys (triangle) in the upper St. Joe River basin, Idaho, during 2022 (upper panel) and 2023 (lower panel). Shapes filled in with black indicate that Bull Trout *Salvelinus confluentus* were present, and hollow shapes indicate Bull Trout were absent. Arrows indicate the location of passive integrated transponder arrays.

tributaries in the upper portion of the St. Joe River basin with the most potential spawning and juvenile rearing habitat. We began field sampling after spring runoff, once streams neared base flow, and ended in the lower portion of the study area before 7 August. Idaho Department of Fish and Game has historically ended all sampling operations in the watershed on 7 August to avoid interfering with adult Bull Trout spawning. However, with approval from IDFG, we were able to sample stream reaches in the study area that were upstream of where 90% of redds had occurred during the previous five spawning ground surveys.

Because little was known about the distribution of Bull Trout in the USJRB, we used a systematic sampling design to select sampling reaches in a manner that would evenly distribute effort and maximize the area sampled during the short sampling season. We divided the mainstem St. Joe River and each tributary into either 200-m (i.e., mainstem St. Joe River) or 100-m (i.e., tributaries) reaches. We randomly chose one of the two most downstream reaches of each stream for sampling and sampled every alternate upstream reach. We partitioned sampling reaches into groups of six. We conducted a multiple-pass depletion survey at the first sampling reach in a group where a Bull Trout was present; we conducted a single-pass survey at the remaining two sampling reaches in the group. If no Bull Trout were encountered at the first two sampling reaches, we conducted a multiple-pass depletion survey at the final sampling reach regardless of the presence of fish to ensure an even distribution of multiple-pass depletion sites within a stream. We continued sampling until fish were not present at multiple reaches in the upper portion of a study stream or there was a barrier that limited fish distribution. We georeferenced all sampling reaches at the downstream terminus of the reach.

We conducted multiple-pass depletion and single-pass surveys using backpack electrofishing units (model LR 24; Smith-Root Inc., Vancouver, WA, USA) to estimate the distribution and abundance of juvenile Bull Trout (Carle and Strub 1978, Ogle 2016, Reynolds and Dean 2020, Meyer et al. 2021). Each multiple-pass depletion survey consisted of at least three passes. If the Bull Trout count on the third pass was >50% of the count for the second pass, we conducted a fourth pass (Meyer and High 2011). We conducted additional passes until the count on the final pass was <50% of the previous pass. Initially, we deployed block nets at the beginning and end of each sampling reach. However, because of the water velocity and riparian characteristics of the streams, we were unable to effectively deploy block nets. Instead, we terminated sampling reaches at the intersection of two channel units (e.g., riffle-pool transition; Young and Schmetterling 2004, Meyer and High 2011). We measured water temperature (°C) and conductivity (µS/cm) before sampling and set the electrofisher setting to 50 Hz and 25% duty cycle. We adjusted voltage until the electrofishing unit produced approximately 100 watts of average power output (Dunham et al. 2009; Reynolds 2012; Meyer et al. 2021). We conducted backpack electrofishing in an upstream direction and sampled all available habitat. We recorded total time in seconds that electricity was applied to water as a measure of sampling effort. Electrofishing was conducted by teams of three individuals for the tributaries and five individuals for the mainstem St. Joe River. We sampled tributaries (i.e., Heller, Medicine, Sherlock, and Wisdom creeks) using a single electrofishing backpack unit. We sampled the mainstem St. Joe River upstream of the confluence with Wisdom Creek following the same protocols as the tributaries because of its relative size. We sampled the mainstem St. Joe River downstream of the confluence to Wisdom Creek using two electrofishing backpack units because of its relatively large size compared to the tributaries.

We netted all fish using dip nets that had 4.8-mm atlas mesh (Duraframe Dipnet, Viola, WI, USA) and placed fish in 18.9-L buckets for temporary holding. We processed fish streamside immediately after capture. Fish were anesthetized with eugenol. We identified fish to species for all genera except sculpin. Morphological similarities make Cedar Sculpin and Shorthead Sculpin exceptionally difficult to identify to species in the field and hereafter are collectively referred to as sculpin (Lemoine et al. 2014). We measured total length (TL) of all fish to the nearest 1.0 mm. We implanted Bull Trout >70 mm TL with a 12-mm half-duplex (HDX) passive integrated transponder tag (PIT tag; Oregon RFID, Portland, OR, USA). We injected PIT tags into the body cavity below the lateral line along an invisible line connecting the distal end of the pectoral fin to the proximal end of the pelvic fin (Achord et al. 1996, Bateman et al. 2009). We ensured the PIT tag was injected in an anterior to posterior direction at an angle that did not interfere with any internal organs or damage the pelvic girdle or lower intestinal track (Vollset et al. 2020). We removed a small portion of the anal fin for genetic analysis. We collected scales from every Bull Trout >70.0 mm TL from the area just posterior to the dorsal fin and dorsal to the lateral line on the left side of the body (Quist et al. 2012, McInerny 2017). Scales collected from fish sampled in 2022 and recaptured in 2023 were collected from the area just posterior to the dorsal fin above the lateral line on the right side of the body. We stored all scales in coin envelopes and later processed them in a laboratory. We placed fish into recovery buckets consisting of water retrieved from the stream. We held fish until full locomotion was restored (~5 min). We released all sampled fish approximately 75 m downstream of the study reach after each pass at sites where we conducted a multiple-pass depletion survey. We released fish directly into the sampling reach when we conducted a single-pass survey.

We evaluated habitat immediately after fish sampling for each reach where we conducted a multiple-pass depletion survey. We categorized channel units as pool, riffle, run, or cascade (Platts et al. 1983, Heckel et al. 2020, Heller et al. 2022) and measured the length of each channel unit in the sampling reach using a laser rangefinder (Leupold Optics, Beaverton, OR, USA) if the channel unit was longer than 7.0 m or a field tape if the channel unit was less than 7.0 m long. We measured wetted width perpendicular to the thalweg at the center of each channel unit. We recorded maximum depth to the nearest 0.1 m for each pool in a sampling reach or at the deepest point of the reach if a pool was not present. We visually estimated substrate composition and substrate embeddedness for each channel unit in the sampling reach using a modified Wentworth scale to categorize substrate as silt, sand, gravel, cobble, or boulder (Wentworth 1922, Heckel et al. 2020). We also visually estimated substrate embeddedness (i.e., 0–5%, 5–25%, 25–50%, 50–75%, 75–100%) at each channel unit using the rating system described by Platts et al. (1983). We measured canopy cover using a spherical concave densiometer at the bottom, middle, and top of the sampling reach (Lemmon 1956). We visually estimated bank characteristics as the proportion of large woody debris, non-woody debris, and bare ground. We considered all wood present greater than 10.0 cm in diameter as large woody debris and wood less than 10.0 cm in diameter and shrubbery as non-woody debris. We considered grasses and bare rock as bare ground. We deployed temperature loggers (HOBO Data Loggers; Onset Inc., Cape Cod, MA, USA) throughout the watershed. We placed temperature loggers in each tributary immediately upstream of the confluence with the St. Joe River. Additionally, we placed at least one logger upstream of the confluence approximately halfway between the mouth of the tributary and the terminus of the sampled portion of the stream, placed another logger at the upper terminus of the sampled portion of the stream, and evenly distributed temperature loggers throughout the mainstem St. Joe River. We programmed all loggers to record stream temperature at 1-h intervals for the entirety of the study period.

Outmigration

We installed five HDX PIT tag antenna arrays in the study area to evaluate downstream movement of Bull Trout in the USJRB (Figure 1). We chose locations near the mouth of tributaries to maximize the probability of detecting outmigrating fish. Ultimately, locations for arrays were dictated by sites where loops of wire could be securely fashioned to the bank and streambed, and where a solar panel would receive sunlight. Arrays consisted of an HDX PIT tag data logger and antenna tuning board (Oregon RFID), three deep-cycle 12-V absorbed glass-mat batteries (Sun Xtender Solar Batteries, West Covina, CA, USA; Duracell Batteries, Bethal, CT, USA), and a 140-W solar panel (Solartech Power, Inc., Ontario, CA, USA). The batteries and data loggers were housed inside 142-L rotomolded waterproof coolers (Grizzly, Decorah, IA, USA), and the solar panel was mounted to a post immediately adjacent to the antenna. We installed half-duplex antenna arrays with a pass-through design (Heller et al. 2022). We operated antenna arrays from late July–October in 2022 and late June–October in 2023 because of restricted access during the winter months. We evaluated the efficiency of antenna arrays at least once per month throughout the study period by placing a PIT tag into a microcentrifuge tube and floating the tube and PIT tag down the thalweg of the stream through the center of the loop of the antenna array 10 times (Zydlewski et al. 2006, Heller et al. 2022). Passive integrated transponder tag array efficiency was consistently 100%.

Laboratory analysis

We removed scales from coin envelopes and pressed them between two glass microscope slides (McInerny 2017). We viewed all scales using transmitted light at 80× magnification with a Leica digital camera (model DMC 2900) and a Leica compound light microscope (model M125; Leica Camera, Wetzlar, Germany). A single reader enumerated annuli and then measured annuli spacing with image analysis software (Image-Pro Plus, Media Cybernetics, Rockville, MD, USA). Genetic samples were processed for sex identification with restriction-site associated DNA (RAD) sequencing on one high-quality single-nucleotide polymorphism (SNP) locus using methods described by Amish et al. (2022) by IDFG staff at the Eagle Fish Genetics Lab in Eagle, Idaho. Genotypes from the sex-identification SNP discovered by Amish et al. (2022) showed 95% agreement with field sex identification.

Data analysis

We estimated absolute abundance of Bull Trout at every reach where a multiple-pass depletion survey occurred. We used the Carle-Strub method using package FSA in statistical software R to estimate abundance (Carle and Strub 1978, R Core Team 2022, Ogle et al. 2023). Because electrofishing is size selective (Reynolds and Kolz 2012), we used only fish >70 mm TL to estimate abundance. We used simple linear regression to evaluate the relationship between absolute abundance estimates and the number of fish caught on the first pass independently for each stream (Meyer et al. 2006; High et al. 2011). The relationship between absolute abundance estimates and the number of fish caught on the first pass generally exhibited a good model fit. One regression had low fit in 2023 (i.e., Sherlock Creek; $r^2 = 0.42$; $P = 0.53$). The remaining streams were similar ($r^2 = 0.63–0.99$; $P = < 0.001–0.05$), with six of the nine remaining regressions having an $r^2 > 0.89$. From this relationship, we estimated the absolute abundance of Bull Trout at sites where we conducted a single pass survey. We estimated Bull Trout abundance at 64 multiple-pass and 136 single-pass reaches in the USJRB in 2022–2023.

We estimated the total abundance and associated variance of Bull Trout in the study area. We considered the total number of sites where a survey was conducted as n and the total number of potential sites that could be sampled as N. We measured the total length of available habitat in each study stream using ArcGIS Pro (Esri, Redlands, CA, USA) to acquire N; we then divided the total length by 100 m for tributaries and 200 m for the mainstem St. Joe River (i.e., sampling reach length for each location; Meyer and High 2006; High et al. 2008). We calculated total abundance estimates for each stream ($\hat{\tau}$) as:

$$\hat{\tau} = \frac{N \sum_{i=1}^{n} y_i}{n},$$

where y_i is Bull Trout abundance for each reach sampled in a stream (Scheaffer et al. 1996). We calculated the associated variance for the total abundance estimate as:

$$V(\hat{\tau}) = N^2 \left(1 - \frac{n}{N}\right)\left(\frac{s^2}{n}\right),$$

where s^2 is the variance of n from a given stream. We summed the total population estimate and associated variances of each stream to produce a total population estimate for the study area.

We tested the difference in mean length at age at capture of Bull Trout sampled in 2022 and 2023 between streams. We conducted Kruskal-Wallis and post hoc pairwise Wilcoxon rank-sum tests ($\alpha = 0.05$) to compare the difference in mean length at age at capture of Bull Trout between streams (Higgins 2004). Additionally, we constructed linear growth models with length at capture as the dependent variable and estimated age of the fish at time of capture (age) as the independent variable. We used the slope (i.e., mm/year) to describe the difference in growth between streams for age-1 through age-3 fish (Quist et al. 2012). We constructed 95% confidence intervals (CIs) for each parameter estimate. We visually examined growth in each tributary and the mainstem St. Joe River using boxplots.

We evaluated the relationship between juvenile Bull Trout abundance and habitat characteristics. We used Spearman's rank correlation coefficient (r_s) to identify multicollinearity between habitat variables (Heckel et al. 2020). We considered variables as highly correlated if the $|r_s|$ for two variables was greater than or equal to 0.70 (Heckel et al. 2020), and we retained the variable with the most ecological importance or management application based on our expert knowledge.

We used regression modeling with a negative binomial distribution (R Core Team 2022; R package, lme4) to evaluate associations of habitat characteristics and abundance at 61 stream reaches. We used residual diagnostic plots and the dispersion parameter ($\hat{c}$; R package, DHARMa) to evaluate overdispersion (Burnham and Anderson 2002, Hartig 2018) and chose a negative binomial distribution because models fit using a Poisson distribution were highly overdispersed (Fisher 1941, Booth et al. 2003). We constructed models in a hierarchical mixed-effects framework with stream (e.g., Heller, Medicine, Sherlock, Wisdom creeks, and the St. Joe River) and year (e.g., 2022, 2023) as random effects, an offset term of $\log_{10}$ reach length (Bates et al. 2015), and 14 candidate variables to evaluate the relationship between Bull Trout abundance and habitat characteristics We developed abundance models using the GLMER.NB function in R (R package, lme4). We examined 26 *a priori* candidate models composed of the 14 variables (additive effects, no interactions) and the null model to evaluate the relationship between juvenile Bull Trout abundance and habitat (Table S1).

We investigated demographic characteristics (i.e., length, sex) associated with outmigration of Bull Trout using logistic regression with the GLM function in R. We evaluated model fit for outmigration characteristic models by calculating McFadden's pseudo-R^2 (McFadden 1974). McFadden's pseudo-R^2 values greater than 0.10 are considered to indicate good model fit, and values greater than 0.20 indicate excellent model fit (Hosmer and Lemeshow 1989). We used three *a priori* candidate models composed of two variables and the null model to evaluate outmigration characteristics (Table S2). We ranked competing regression models using Akaike's Information Criterion adjusted for a small sample size (AIC_c; Burnham and Anderson 2004). We considered all models with a ΔAIC_c value less than two as plausible.

RESULTS

Distribution and abundance

We sampled 17,537 fish in the USJRB in 2022–2023, including 1,529 Bull Trout, 2,152 Westslope Cutthroat Trout, 20 Kokanee, and 13,789 sculpin. Bull Trout were present at 153 of the 200 (77%) reaches sampled across years (Figure 1). Bull Trout were most frequently sampled in Medicine Creek (94% of reaches), followed by the St. Joe River (81%), Wisdom Creek (74%), Heller Creek (68%), and Sherlock Creek (18%). Westslope Cutthroat Trout were common throughout the mainstem St. Joe River and three of the tributaries (e.g., Heller, Wisdom, Sherlock creeks). We sampled a single Westslope Cutthroat Trout in Medicine Creek in 2022. Sculpin were common throughout the study area and were present in the mainstem St. Joe River and all study tributaries. Distribution of sculpin mirrored the distribution of Bull Trout throughout the study area except for the uppermost 1.8 km of Wisdom Creek where we did not sample a sculpin either year. We sampled Kokanee in the mainstem St. Joe River in both years. This was the first record of a nonnative fish species in the designated Wild and Scenic portion of the St. Joe River. We sampled the highest numbers of Bull Trout of all ages in Medicine Creek (2022 = 169, 2023 = 517), followed by the mainstem St. Joe River (240, 263), Wisdom Creek (104, 138), Heller Creek (63, 28), and Sherlock Creek (1, 5). We estimated total abundance for juvenile Bull Trout between 70 – 260 mm TL in the study area to be 1,841 (95% CI = 1,187.8–2,494.2) in 2022 and 2,388 (1,645.8–3,130.2) in 2023. Medicine Creek had the highest density of Bull Trout in both years of the study; whereas, Sherlock Creek had the lowest densities of Bull Trout (Table 1).

Habitat characteristics and associations

Habitat characteristics across streams exhibited several differences (Table 2). For instance, Medicine and Wisdom creeks typically had the highest channel gradient (>2.5%). They also had the lowest mean daily water temperatures (<8°C), highest percentage of canopy cover (>40%), and the most large woody debris (>40%) of the study streams. In contrast, Heller and Sherlock creeks typically had the lowest canopy cover (<15%) of the study streams. Additionally, Heller and Sherlock creeks had little large woody debris and higher mean daily water temperatures (10–11°C) compared to other streams. All the streams were dominated by riffle-run habitats. Medicine Creek had the highest percentage of pools; cascade habitat was relatively common in Wisdom Creek and generally absent from other streams. We identified four top models evaluating the relationship between Bull Trout abundance and habitat characteristics, and retained a single top model evaluating demographic characteristics of outmigration. Regression modeling suggested that Bull Trout abundance in the USJRB was positively related to canopy cover, percent boulder substrate, the amount of large woody debris, and percent gravel, and inversely related to mean daily water temperature (Table 3).

TABLE 1 Mean total length (mm), minimum total length (mm), maximum total length (mm), and standard deviation of Bull Trout *Salvelinus confluentus* sampled in the upper St. Joe River basin, Idaho, in 2022–2023. We provide abundance estimates for each stream with lower and upper confidence intervals and density estimates (Bull Trout/100 m).

Stream	*n*	Min	Max	Mean	SD	Abundance estimate	Lower CI	Upper CI	Density
2022									
St. Joe River	240	40	257	121	40	693.4	464.7	922.0	4.5
Heller Creek	63	38	203	117	32	247.5	168.6	326.5	4.8
Sherlock Creek	1	84	84	84	0	4.8	−4.4	13.9	0.1
Medicine Creek	169	34	191	120	35	480.9	348.9	612.8	13.0
Wisdom Creek	104	40	227	135	41	414.3	196.3	632.2	9.6
2023									
St. Joe River	263	45	246	132	40	690.5	508.7	872.3	4.5
Heller Creek	28	38	181	114	43	111.7	78.3	145.1	2.1
Sherlock Creek	5	140	243	165	40	43.0	19.7	66.3	1.0
Medicine Creek	517	29	234	76	30	1,175.4	821.0	1,529.8	31.7
Wisdom Creek	138	44	215	126	48	367.2	202.6	531.7	8.5

TABLE 2 Mean and standard deviation (in parentheses) of abiotic variables measured from 62 reaches in the mainstem St. Joe River and four tributaries (Heller, Medicine, Sherlock, Wisdom creeks) in Idaho in 2022–2023. Measurements were used as explanatory variables in candidate models to evaluate the habitat associations of juvenile Bull Trout *Salvelinus confluentus* in the upper St. Joe River basin.

Variable	Description	St. Joe River	Heller Creek	Medicine Creek	Sherlock Creek	Wisdom Creek
Gradient	Reach length divided by the elevation change (%)	1.6 (1.4)	1.6 (1.5)	2.7 (2.1)	1.9 (1.1)	3.2 (2.9)
Temperature	Mean daily stream temperature during August	10.7 (0.9)	9.7 (0.6)	7.1 (0.5)	10.5 (0.3)	7.9 (1.2)
Runs	Proportion of reaches as run (%)	30.4 (16.3)	25.7 (21.9)	35.8 (22.9)	41.0 (20.3)	21.4 (17.1)
Riffle	Proportion of reaches as riffle (%)	58.7 (20.4)	66.4 (19.8)	44.6 (29.0)	47.6 (18.1)	51.5 (30.3)
Pool	Proportion of reaches as pool (%)	6.4 (9.1)	7.8 (6.8)	14.0 (8.5)	11.6 (9.4)	11.1 (10.7)
Cascade	Proportion of reaches as cascade (%)	4.6 (20.8)	0.0 (0.0)	4.6 (10.3)	0.0 (0.0)	16.0 (33.7)
Maximum depth	Maximum water depth (m)	0.8 (0.3)	0.6 (0.2)	0.6 (0.1)	0.7 (0.4)	0.7 (0.2)
Canopy cover	Mean canopy cover (%)	23.0 (16.4)	8.2 (2.6)	53.5 (9.7)	13.0 (8.6)	44.5 (12.8)
Boulder substrate	Proportion of channel units with dominant substrate type boulder (%)	27.0 (37.9)	24.3 (26.5)	9.4 (15.9)	3.2 (7.2)	37.6 (37.9)
Gravel substrate	Proportion of channel units with dominant substrate type gravel (%)	1.0 (2.6)	0.4 (1.4)	13.5 (16.3)	4.0 (8.9)	3.9 (0.6)
Embeddedness	Proportion of substrate that is covered in silt and sand	3.7 (0.9)	4.6 (0.5)	4.2 (0.6)	3.6 (0.55)	36.6 (3.0)
Proportion large woody debris	Proportion of large woody debris (%)	20.5 (7.8)	19.4 (12.3)	43.4 (12.3)	22.8 (17.1)	39.8 (11.8)
Proportion non-woody debris	Proportion of non woody debris (%)	39.6 (11.8)	58.4 (13.9)	40.8 (18.9)	35.4 (10.7)	36.7 (19.5)
Proportion bare ground	Proportion of bare ground (%)	39.9 (11.8)	22.8 (8.6)	16.9 (15.8)	42.0 (24.4)	22.5 (13.8)

TABLE 3 Regression models used to evaluate habitat associations of juvenile Bull Trout *Salvelinus confluentus* in the upper St. Joe River basin, Idaho, in 2022–2023. Models were ranked using Akaike's Information Criterion adjusted for a small sample size (AIC_c). We retained models within two AIC_c of top model as top models, and we report the best five models. Difference in AIC_c (ΔAIC_c), model weight (w_i), and R^2 are included. Direction of effect for each covariate is indicated ([+] positive, [−] negative). Abundance models include a random effect term for year and stream and an offset term of $\log_{10}$ reach length.

Model	AIC_c	ΔAIC_c	w_i	R^2
+ canopy cover + large woody debris	388.0	0.0	0.17	0.50
+ canopy cover + large woody debris – temperature + boulder	388.8	0.8	0.11	0.53
+ canopy cover + boulder	389.2	1.3	0.09	0.46
+ canopy cover + large woody debris + gravel	389.6	1.6	0.07	0.50
+ canopy cover – temperature + large woody debris	390.2	2.2	0.06	0.50

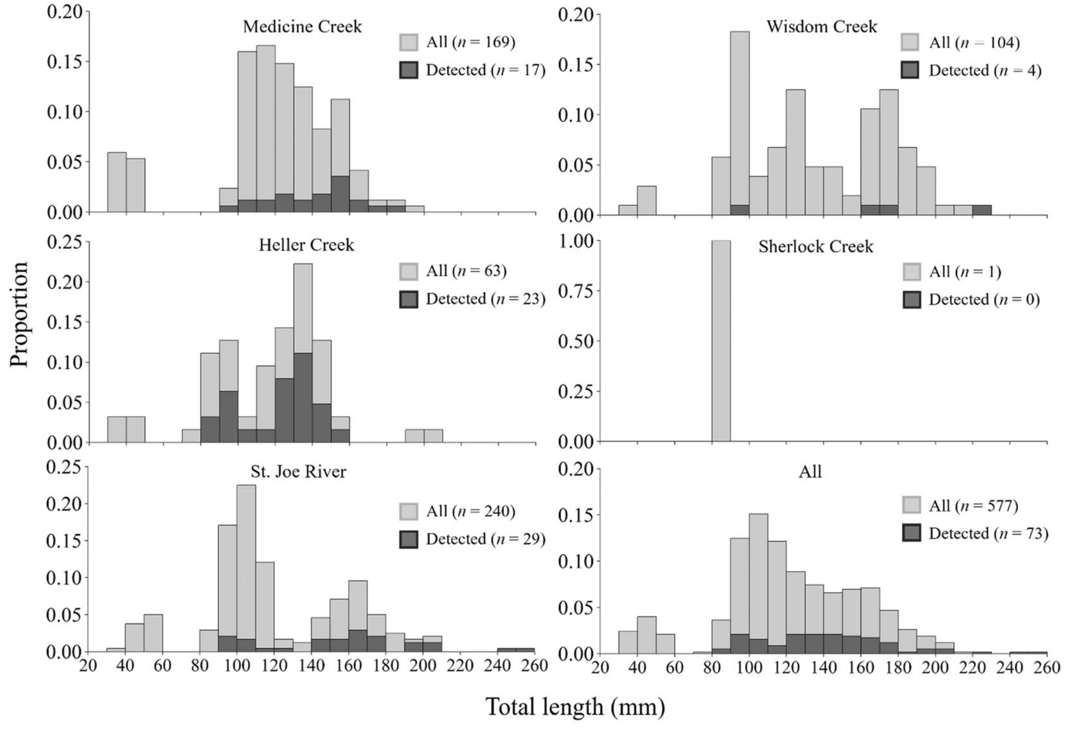

FIGURE 2 Length structure of Bull Trout *Salvelinus confluentus* sampled in the upper St. Joe River basin, Idaho, in 2022. Light grey bars represent all Bull Trout sampled. Dark grey bars represent Bull Trout that were detected moving by stationary passive integrated transponder arrays.

Length, age structure, and growth

Total length of Bull Trout sampled during the study varied from 29 – 257 mm TL (Table 1; Figures 2 and 3). Average length of Bull Trout sampled in 2022 (mean ± SD; 123 ± 39 mm TL) was similar to 2023 (100 ± 45 mm TL). Mean length varied slightly within and between streams in 2022–2023 (Table 1). We did not observe evidence for a

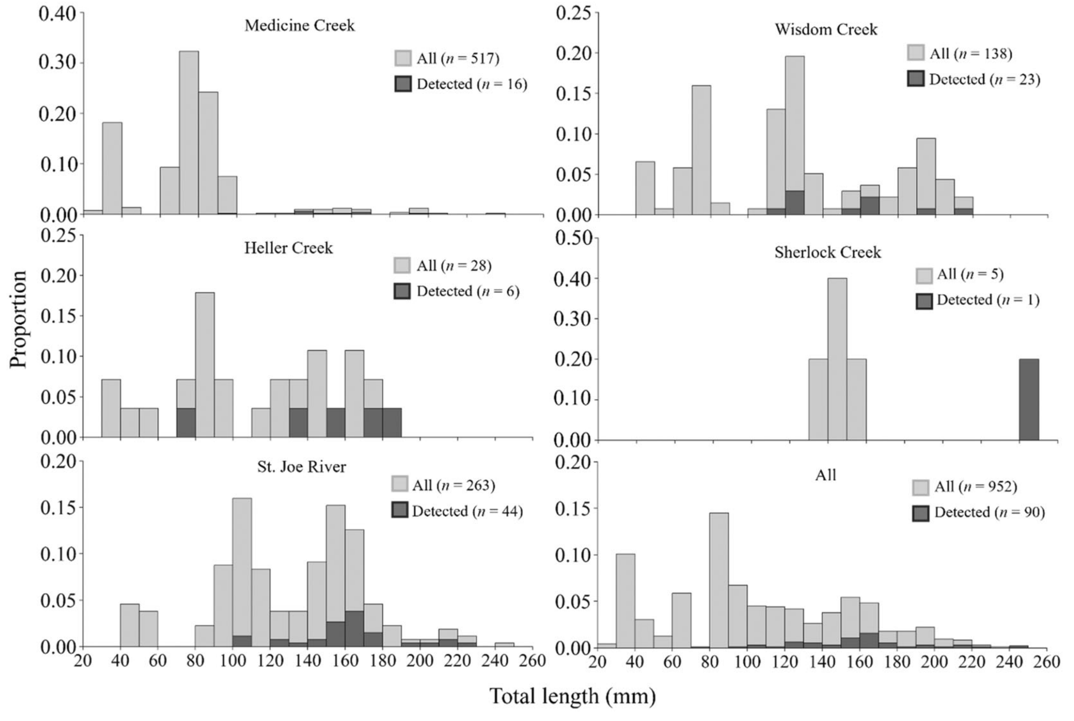

FIGURE 3 Length structure of Bull Trout *Salvelinus confluentus* sampled in the upper St. Joe River basin, Idaho, in 2023. Light grey bars represent all Bull Trout sampled. Dark grey bars represent Bull Trout that were detected moving by stationary passive integrated transponder arrays.

difference in mean total length of Bull Trout between streams in 2022 ($W = 28–57$; $P = 0.17–0.99$). In 2023, Bull Trout sampled in Medicine Creek (mean ± SD; 76 ± 30 mm TL) were smaller than in all other streams ($W = 14$, $P < 0.001$). We did not find evidence that mean length of Bull Trout sampled in all other streams in the study area differed (mean ± SD; 126 ± 41 mm TL; $P > 0.05$) in 2023.

Estimated ages from all Bull Trout sampled in the study area varied from 1 to 3 years in 2022 and 1 to 4 years in 2023 (Figure 4). In 2023, mean lengths at age at capture were approximately 21–26 mm shorter at each age compared to 2022 (Table 4). Growth of age-1 to age-3 Bull Trout varied slightly between sampling streams in 2022–2023 (Figure 5). Sex ratio (female:male) for age-1 and age-2 Bull Trout combined was 47:53 ($n = 1{,}065$), whereas the sex ratio for age-3 and age-4 fish was 28:72 ($n = 92$).

Outmigration characteristics

We PIT tagged 1,142 Bull Trout varying in length from 71 – 257 mm TL (mean length ± SD; 125 ± 39 mm TL) over the course of the study. Of the tagged Bull Trout, 163 (14%) were detected by a stationary PIT tag array between June through October in both years (Figure 6). The proportion of PIT-tagged individuals detected outmigrating was highest in Heller Creek (35%), followed by Sherlock Creek (33%), the mainstem St. Joe River (16%), Wisdom Creek (12%), and Medicine Creek (8%). The mean total length of all fish detected on a stationary PIT-tag array was 15% greater than the mean length of all Bull Trout PIT tagged, but this difference varied between streams (Figure 7). Tagged Bull Trout varied in age from 1–4 years and all ages were detected outmigrating. The average length of fish detected compared to all of those PIT tagged was slightly greater for all age classes (Figure 8). Heller Creek had the highest proportion of age-1 fish outmigrate (69%), whereas the mainstem St. Joe River had the highest proportion of age-2 and older fish

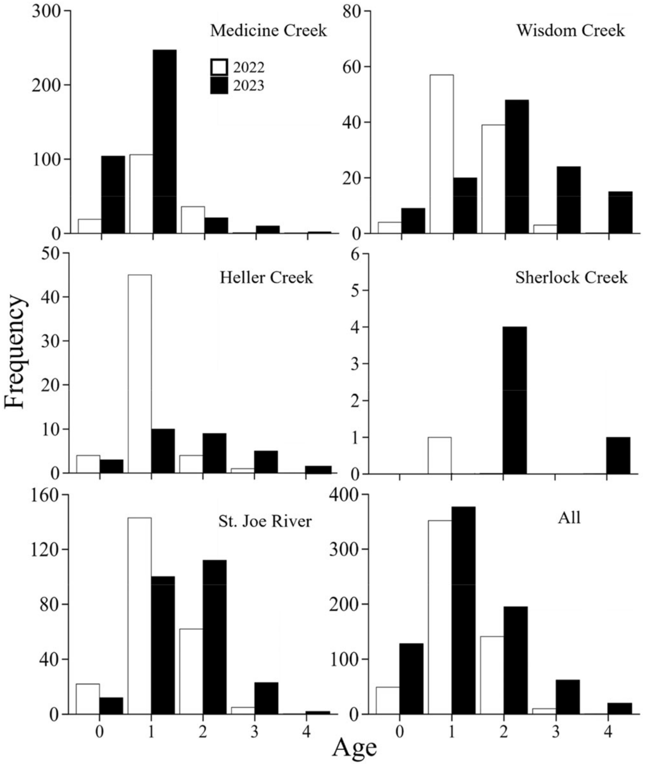

FIGURE 4 Age structure of Bull Trout *Salvelinus confluentus* sampled in the upper St. Joe River basin, Idaho, during 2022–2023.

TABLE 4 Mean total length at age at capture (mm) and standard deviations of age-1 through age-4 juvenile Bull Trout *Salvelinus confluentus* sampled in the upper St. Joe River basin, Idaho, during 2022–2023.

Age	Mean	SD
2022		
1	113	17
2	167	17
3	211	25
2023		
1	90	14
2	146	19
3	185	18
4	203	17

outmigrate (73%). Medicine and Wisdom creeks were intermediate with 41% and 44% of the Bull Trout detected outmigrating being age 1, respectively. Regression modeling suggested that length was the most important variable contributing to outmigration (Table 5). The sex ratio (female:male) for all Bull Trout detected moving was 70:73 and did not exceed more than a 1% difference for each age class other than age 4, which was 1:2 (n = 3). The skewed sex ratio of age-4 outmigrants was likely a function of the overall sex ratio of age-4 Bull Trout in the system.

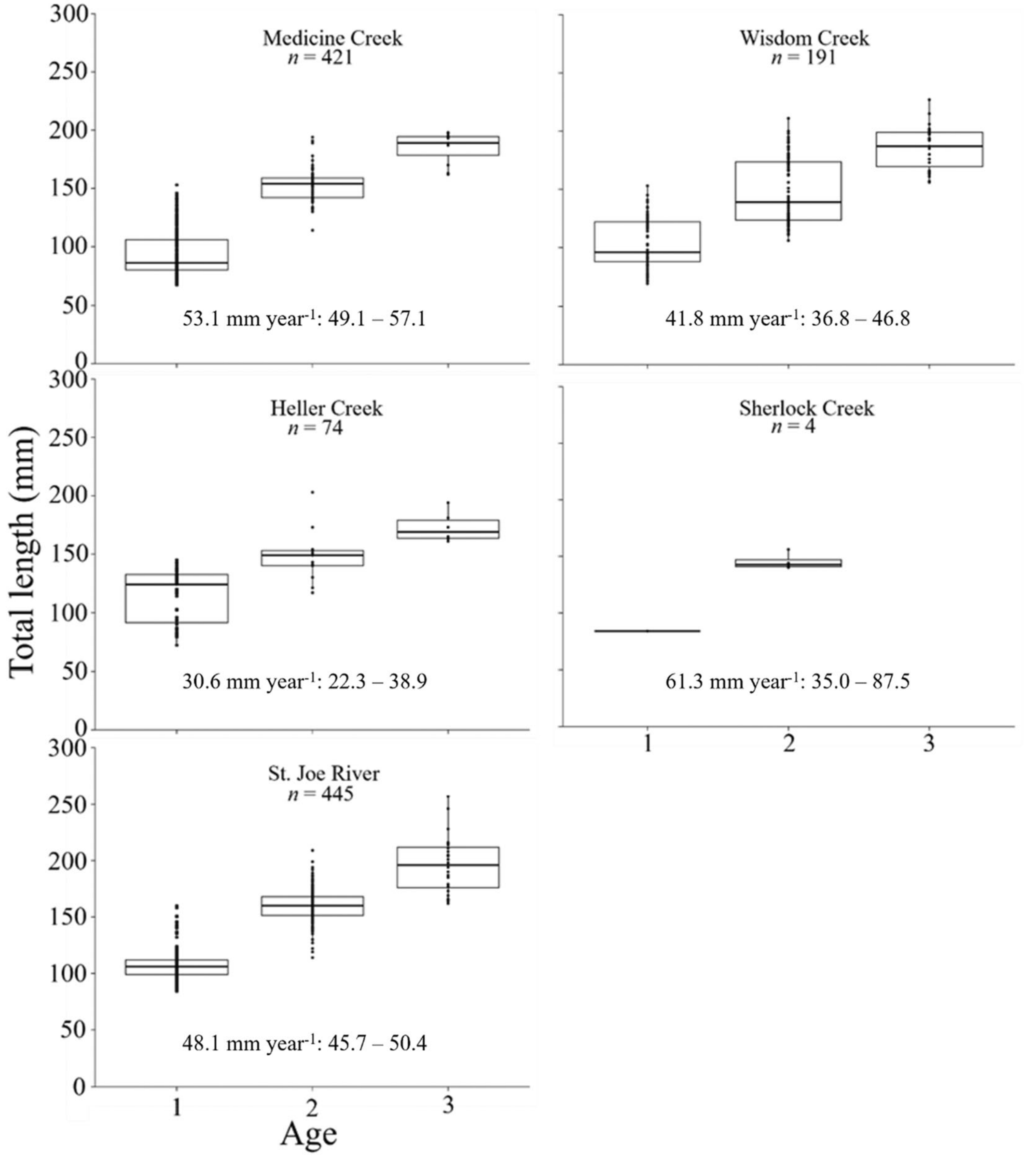

FIGURE 5 Mean length at age at capture and growth increments and 95% confidence intervals of age-1 through age-3 juvenile Bull Trout *Salvelinus confluentus* sampled in the upper St. Joe River basin, Idaho, during 2022–2023.

DISCUSSION

Successful conservation and recovery of fish populations requires a thorough understanding of the population's distribution, abundance, and dynamics. Previous to this study, little was known about Bull Trout in the USJRB beyond observing that adult spawning activity has decreased rapidly since 2008. Although the low production and recent decline in redd abundance may be associated with conditions downstream (Walrath et al. 2015, 2015), a logical location to start initial investigations was in the headwaters. Thus, the primary purpose of this project was to

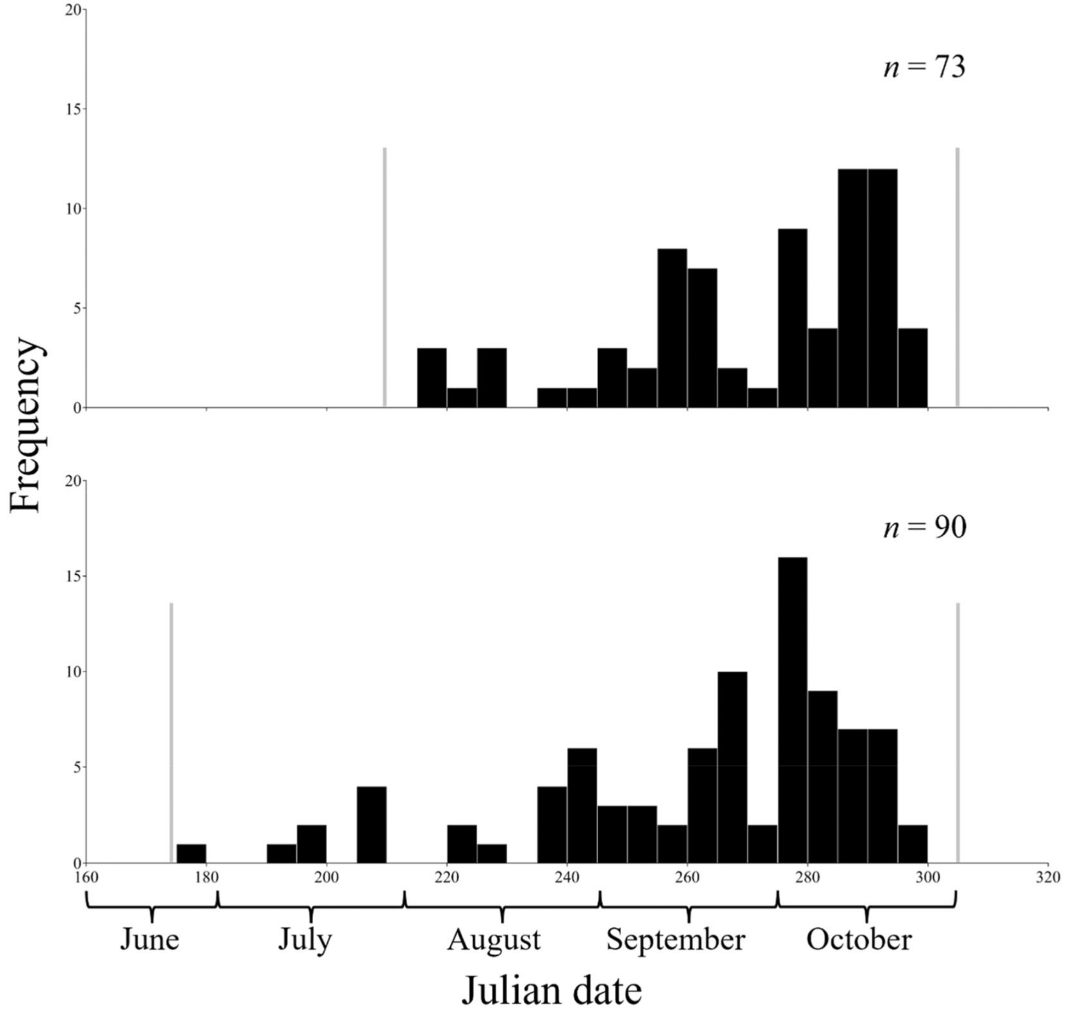

FIGURE 6 Dates when passive integrated transponder (PIT)-tagged Bull Trout *Salvelinus confluentus* were detected moving by a stationary PIT tag array in the upper St. Joe River basin, Idaho, during 2022 (upper panel) and 2023 (lower panel). Vertical gray line indicates when the stationary PIT tag arrays were active.

evaluate the population demographics and dynamics of the juvenile component of the CDACA population in the USJRB.

Since first proposed for listing under the U.S. Endangered Species Act in 1992, substantial effort has focused on increasing knowledge of Bull Trout ecology, including efforts to identify factors associated with the occurrence and abundance at multiple spatial scales (Rieman and McIntyre 1993, 1995; Rieman et al. 1997; Rieman and Allendorf 2001; Al-Chokhachy et al. 2010). The densities of juvenile Bull Trout we observed in the USJRB are comparable to those observed in tributaries to Lake Pend Oreille, Idaho, despite the drastic difference in adult abundances between the two systems. Bull Trout densities in tributaries to Lake Pend Oreille have averaged 7.8 Bull Trout/100 m since 2012 (Avista and Idaho Department of Fish and Game, unpublished data). The highest densities observed in that period were in Granite Creek (i.e., 28.5 Bull Trout/100 m), which are less than the density observed in Medicine Creek in 2023 (i.e., 31.7 Bull Trout/100 m). Furthermore, in tributaries to the Clark Fork River, Montana, Lewis (2021) observed average densities of age-1 and older juveniles of 25.7 Bull Trout/100 m (i.e.,

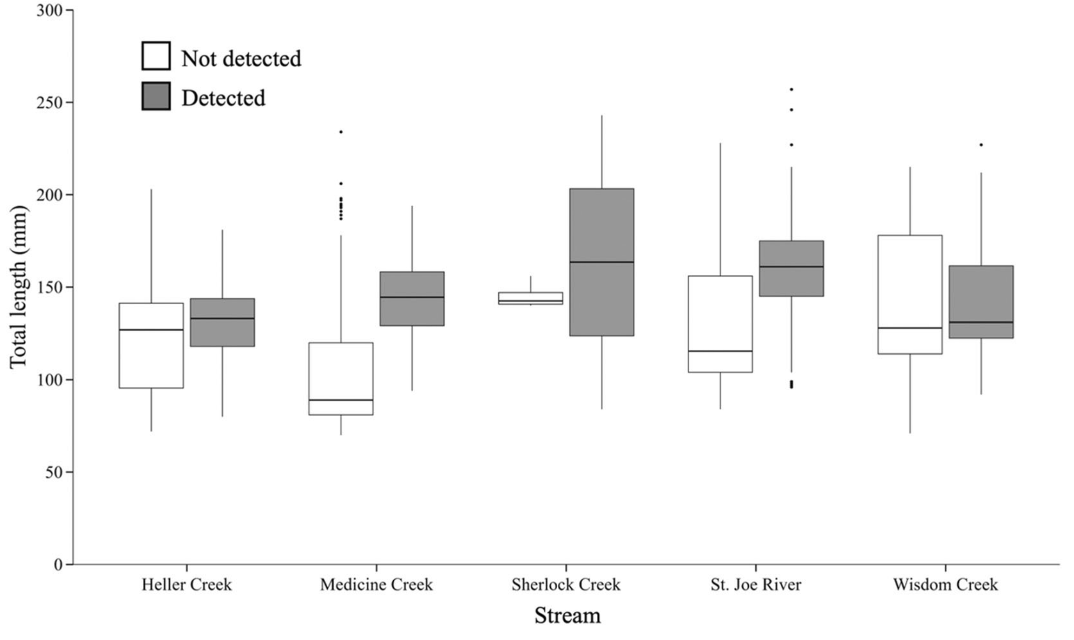

FIGURE 7 Mean length of passive integrated transponder (PIT)-tagged Bull Trout *Salvelinus confluentus* detected by stationary PIT tag arrays and mean length of PIT-tagged Bull Trout not detected by stationary PIT tag arrays in the upper St. Joe River basin, Idaho, during 2022–2023.

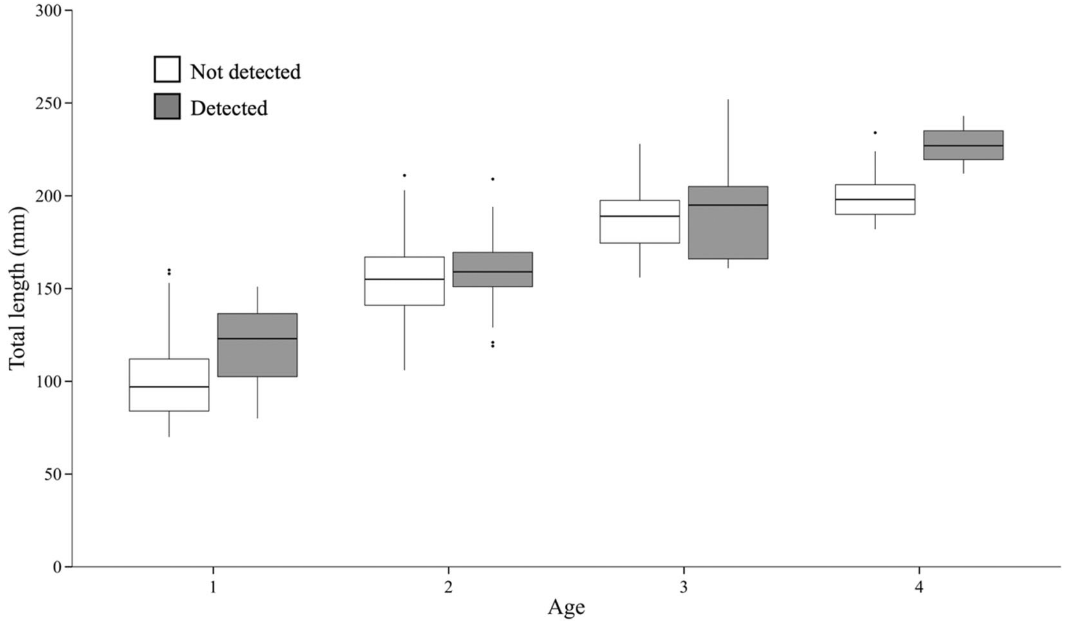

FIGURE 8 Mean length at age at capture of passive integrated transponder (PIT)-tagged Bull Trout *Salvelinus confluentus* detected by stationary PIT tag arrays compared to PIT-tagged Bull Trout not detected in the upper St. Joe River basin, Idaho, during 2022–2023.

TABLE 5 Regression models used to evaluate the probability of outmigration of juvenile Bull Trout *Salvelinus confluentus* in the upper St. Joe River basin, Idaho, in 2022–2023. Models were ranked using Akaike's Information Criterion adjusted for a small sample size (AIC_c). We retained models within two AIC_c of top model as top models and report models within 10 AIC_c. Difference in AIC_c (ΔAIC_c), model weight (w_i), and McFadden's pseudo-R^2 (R^2) are included. Direction of effect for each covariate is indicated ([+] positive, [−] negative).

Model	AIC_c	ΔAIC_c	w_i	R^2
Length	894.3	0.0	0.83	0.11
Length + sex	897.5	3.2	0.17	0.09

Graves Creek) and 10.2 Bull Trout/100 m (i.e., East Fork Bull River) in 2019–2020. Previous research efforts have shown that Bull Trout occurrence and abundance are often associated with deep, low-velocity habitat (e.g., pools, deep runs; Rieman and McIntyre 1993, 1995; Al-Chokhachy et al. 2010). Streams in our study were dominated by riffle-run habitats, but Medicine Creek had the highest percentage of pools and the highest densities of Bull Trout. In contrast, the stream with the second-highest average depth (i.e., Sherlock Creek) had the lowest density of Bull Trout in the study. However, average reach depth in Sherlock Creek was a byproduct of impoundment from numerous beaver *Castor canadensis* dams, which were not common in other streams. Although deep, low-velocity habitat is important for Bull Trout, our results suggest that other habitat variables (e.g., large woody debris, canopy cover) were also important for the occurrence and abundance of juveniles in the USJRB.

The proportion of large woody debris present at the two streams with the highest Bull Trout densities (i.e., Medicine Creek, Wisdom Creek) was greater than that observed in streams with lower densities (Heller Creek, Sherlock Creek, St. Joe River). Bonneau and Scarnecchia (1998) found that juvenile Bull Trout used large substrate and large woody debris as cover in over 75% of their observations during a study of habitat use in tributaries to Lake Pend Oreille. In 18 watersheds throughout Washington, Idaho, and Montana, occurrence was more frequent in V-shaped valleys with large woody debris cover compared to alluviated lowlands with moderate amounts of large woody debris (Watson and Hillman 1987). The amount of large woody debris in Sherlock Creek was not much different from that in Medicine and Wisdom creeks, but Sherlock Creek generally lacked large substrate and is in a less confined, U-shaped valley. In addition to channel-unit complexity created by the presence of large woody debris and large substrate, Bull Trout occurrence and abundance have also been related to canopy cover (Rieman and McIntyre 1993). Although canopy cover cannot be completely disconnected from large woody debris, the way canopy cover likely affects abundance is slightly different. Canopy cover provides protection from overhead predators (i.e., osprey *Pandion haliaetus*) and mitigates stream temperatures (Penaluna et al. 2016). We found that the two streams with low canopy cover (i.e., Heller and Sherlock creeks) had the lowest densities in the study area. Additionally, a study investigating juvenile Bull Trout in the upper Payette River, Idaho, revealed positive associations with canopy cover and Bull Trout occurrence (Zurstadt 2000, Al-Chokhachy et al. 2010).

Stream temperature is typically considered an important factor associated with the occurrence of Bull Trout (McMahon et al. 2007, Al-Chokhachy et al. 2010, Benjamin et al. 2016). Observational studies in a natural environment have shown that occurrence is rare when maximum temperatures exceed 15.0°C (Fraley and Shepard 1989, Isaak et al. 2012, Jones et al. 2014). Even at a relatively small spatial scale, abundance was inversely related to temperature in the USJRB. The two streams (i.e., Medicine and Wisdom creeks) with the highest densities of Bull Trout had the lowest August temperatures (<8.0°C), whereas the streams with the warmest August temperatures (Heller and Sherlock creeks) had the lowest densities. Furthermore, reaches in the mainstem St. Joe River with the highest densities of Bull Trout were farther upstream in the study area, where stream temperatures were relatively colder compared to lower reaches. However, mean August temperatures throughout the study area were within the fundamental thermal niche of Bull Trout (8.0 – 13.9°C; Selong et al. 2001) and lower than what has been observed in streams with higher densities (Benjamin et al. 2016), suggesting that a lack of thermal refuge is likely not a limiting factor in the study area.

Age structure was dominated by age-1 and age-2 individuals in the USJRB. Sex ratio for age-1 and age-2 Bull Trout combined was similar between females and males, whereas the sex ratio for age-3 and age-4 fish combined was skewed towards males (i.e., 28:72). Two mechanisms could be responsible for the difference in sex ratios. Females could have higher mortality at younger ages compared to their male counterparts. However, mechanisms that would result in sex-biased juvenile mortality are not obvious. More likely, females may leave the system at a younger age than males. Sex-biased differences in age at outmigration and outmigration timing in salmonid populations have been observed (Nagara and Irvine 1997; Thompson et al. 2015). Nagara and Irvine (1997) found that female juvenile Masu Salmon *Oncorhnchus masou* were two times more likely to move out of natal spawning streams compared to males in the upper Shiribetsu River and Atsuta River basins in Japan. Early migration to habitats that promote increased growth rates (e.g., marine or lentic systems) compared to less productive natal streams could benefit females by increasing relative fitness because fecundity is directly related to length in salmonids (Wedekind and Műller 2004). Whether similar mechanisms are occurring in the USJRB is unknown but could be an area of future investigation.

Growth provides an integrated measure of environmental conditions that can provide important insight into habitat quality. The growth rates of juvenile Bull Trout observed during our study are similar to those observed in other studies evaluating growth of juveniles from migratory populations (Al-Chokhachy and Budy 2008; McCubbins 2013). Growth of Bull Trout varying in length from 120 − 170 mm TL was approximately 53.6 mm/year in the South Fork Walla Walla River, Oregon (Al-Chokhachy and Budy 2008). This growth rate is similar to the overall growth rate we observed in the USJRB. Furthermore, growth of age-1 through age-3 Bull Trout was 76.0 mm/year in tributaries to Lake Pend Oreille (McCubbins 2013). Although these growth rates were ~28 mm greater than what we observed, average stream temperature in Lake Pend Oreille tributaries was 3°C higher than the average stream temperature in our study streams (i.e., 9.2°C). The relatively high growth rate in Medicine Creek compared to the other streams may reflect high production of prey resources (Rosenfeld and Taylor 2009, Gustafsson et al. 2014). Medicine Creek had the highest proportion of large woody debris of any of the study streams. Behnke et al. (1984) found that the diversity and abundance of invertebrate fauna were greater in streams with abundant woody debris compared to less-complex stream reaches with little large woody debris.

Prior to our study, little was known about the outmigration characteristics of Bull Trout in the basin. Migratory behavior is often highly variable within and between stream systems (Rieman and McIntyre 1993). In other systems, outmigrating juvenile Bull Trout have varied from age 0 to age 4 (Fraley and Shepard 1989, Downs et al. 2006, Lewis et al. 2022). Bull Trout in the Metolius River system, Oregon, outmigrated from natal streams to Lake Billy Chinook at age 2 and age 3 (Ratliff 1992, Ratliff et al. 2015). Fraley and Shepard (1989) observed that age-1 through age-4 Bull Trout outmigrated in the Flathead River system, Montana, but most (81%) were age 2 and age 3. We detected the highest proportion moving out of Heller and Sherlock creeks, whereas Medicine Creek had the lowest proportion of outmigrating Bull Trout. Movement of age-1 through age-4 Bull Trout was detected in our study, but the majority of outmigrating individuals were age 1 and age 2. We observed a positive relationship between total length at age and the probability of outmigration. In other systems, adult Bull Trout that successfully return to spawn generally outmigrate at older ages (Downs et al. 2006, Zymonas 2006). Resource availability balanced with the risk of outmigration determines the optimal age at outmigration in each system (Thorpe 1994, Paul et al. 2000, Ratliff et al. 2015). Increased migratory survival of individuals that outmigrate at larger sizes could be due to greater energetic reserves or reduced mortality due to downstream predators (Pavlov et al. 2007, Kendall et al. 2015).

An important limitation of our study is that inferences associated with outmigration are limited to late summer and autumn movement on a relatively small number of fish. The remote location and pronounced winter snowpack that occur in the study area created insurmountable logistical constraints to maintaining PIT tag arrays. In 2022, the study area could not be accessed until early July because of snowpack and was inaccessible because of snow by 1 November. In 2023, we were able to access the study area nearly one month earlier, but roads were no longer accessible by 1 November. Thus, stationary PIT tag arrays were operational from July through October in 2022 – 2023. Movement of Bull Trout in the system was detected throughout the late summer and autumn but peaked in October in both years. Considering the low proportion of Bull Trout tagged that were detected on stationary PIT arrays and the low proportion of individuals recaptured in 2023, spring outmigration is likely occurring in the USJRB. Spring outmigration of juvenile Bull Trout has been observed in other populations (Bellerud et al. 1997, Downs et al. 2006). Juvenile Bull Trout have also been found to demonstrate bimodal (spring and autumn) distributions of outmigration (Bellerud et al. 1997, Downs et al. 2006, Lewis et al. 2022). An evaluation focused on outmigration in lower portions of the basin that are more accessible in the spring and winter could provide insight into whether a spring outmigration is occurring in the USJRB.

This is the first study we are aware of to comprehensively document the distribution, abundance, age and length structure, dominant habitat associations, and outmigration characteristics of juvenile Bull Trout in the USJRB in Idaho. Results of our research have implications for conservation of Bull Trout in the CDACA and similar montane ecosystems. The similar densities of juvenile Bull Trout in more productive systems (e.g., Clark Fork River, Lake Pend Oreille tributaries) compared to the USJRB indicate that the CDACA population is likely not limited by juvenile recruitment in the headwater streams.

Investigating how juvenile Bull Trout are distributed throughout the USJRB provides valuable insight into which tributaries and portions of the St. Joe River are being used for rearing habitat. Further research on the timing of outmigration and movement patterns in downstream portions of the migratory corridor would likely provide additional insight into factors limiting production in the CDACA. Although inherently difficult, a comprehensive diet analysis of nonnative predatory fish species in the inundated portions of the St. Joe River and Coeur d'Alene Lake could indicate if predation is limiting production. At a minimum, preserving the intact and relatively unaltered near-stream habitat in the headwaters of the USJRB is important for Bull Trout recruitment.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This project was conducted under protocol 2021-80 approved by the Institutional Animal Care and Use Committee at the University of Idaho.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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