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ARTICLE

Occurrence, Abundance, Movement, and Habitat Associations of Bonneville Cutthroat Trout in Tributaries to Bear Lake, Idaho–Utah

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Abstract
Bonneville Cutthroat Trout (BCT) *Oncorhynchus clarkii utah* in Bear Lake, Idaho–Utah, is an important endemic and recreational species and plays a vital ecological role in systems throughout the basin. Although the distribution and abundance of BCT have declined due to anthropogenic disturbances, production of wild BCT in Bear Lake has increased over the past decade as a result of extensive habitat improvement in spawning tributaries. The objective of this study was to assess the occurrence, distribution, and out-migration of BCT in tributaries of Bear Lake. Surveys were conducted at 75 stream reaches across three study streams (i.e., St. Charles, Fish Haven, and Swan creeks) during 2019 and 2020. A total of 1,064 BCT was sampled from 55 of 75 total reaches (73%). Total length of BCT varied from 22 to 650 mm, and the average TL was 117 mm (SE = 2.2). Regression models were used to identify abiotic and biotic features associated with BCT distribution, abundance, and probability of out-migration. Regardless of the tributary, elevation was negatively related to BCT occurrence and relative abundance. Other habitat characteristics associated with the presence and abundance of BCT were similar to those of other Cutthroat Trout species. For example, BCT were often associated with large substrates, instream cover, canopy cover, and heterogeneity in several habitat characteristics. The probability of a BCT out-migrating was positively associated with fish length and age but negatively related to distance to Bear Lake and number of downstream irrigation diversions. Results from this study provide critical information on the ecology and early life history characteristics of BCT that can be used to guide additional conservation and management efforts (i.e., removal of nonnative fish species; continued habitat restoration efforts).

The Cutthroat Trout *Oncorhynchus clarkii* is an ecologically and socially important species that has a widespread distribution in North America (Behnke 1992, 2002; Budy et al. 2019). Bonneville Cutthroat Trout (BCT) *O. clarkii utah* is one of 14 subspecies of Cutthroat Trout and is native to the Bonneville Basin of Idaho, Nevada, Utah,

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and Wyoming (Behnke 2002). It is a subspecies that warrants protection and conservation due to its importance in many aquatic ecosystems as well as its value as a recreational species (Behnke and Zarn 1976; Trotter 1987; Duff 1988; Berg and Hepworth 1992; Lentsch et al. 2000). Bonneville Cutthroat Trout inhabit both lentic and lotic systems across a variety of elevations, habitat types, and levels of productivity (Schrank and Rahel 2002; Burnett 2003; Colyer et al. 2005; Teuscher and Capurso 2007), and they exhibit two major life history forms: migratory (i.e., adfluvial, fluvial) and nonmigratory (i.e., resident).

Historically, BCT populations existed in 14% (1,447 km) of lotic and lentic systems in the Bonneville Basin (Teuscher and Capurso 2007). As of 2007, BCT occupied only 35% of this historical distribution. In response to the decline in distribution and abundance, BCT was petitioned for listing under the Endangered Species Act in 1998. The U.S. Fish and Wildlife Service determined that a listing for BCT was not warranted at that time because genetically pure populations still existed in numerous tributaries and because several projects aimed at BCT conservation were planned. Despite the decision against Endangered Species Act listing, BCT is considered a sensitive species by the U.S. Forest Service and Bureau of Land Management and is considered a species of high conservation priority by the states of Idaho and Utah. Furthermore, BCT is protected under a multi-partner conservation agreement and is the focus of a subspecies-specific management plan (UDWR 2019).

Bonneville Cutthroat Trout is the only species of trout endemic to the Bonneville Basin, including Bear Lake. Bear Lake is a natural, oval-shaped lake that is bisected by the Idaho–Utah border and is currently managed by both Idaho Department of Fish and Game (IDFG) and Utah Division of Wildlife Resources (UDWR). The population of BCT in Bear Lake is recognized as a relatively distinct subpopulation (Wurtsbaugh and Hawkings 1990; Teuscher and Capurso 2007). Bonneville Cutthroat Trout over 225 mm are predominantly piscivorous, feeding mainly on endemic Bear Lake Sculpin *Cottus extensus* and Bonneville Cisco *Prosopium gemmifer* (Kershner 1995). Additionally, BCT in Bear Lake represent the last remaining population in Idaho that follows an adfluvial life history strategy (Wurtsbaugh and Hawkins 1990; Behnke 1992; Teuscher and Capurso 2007). Four natural tributaries flow into the lake and remain connected in most years: St. Charles and Fish Haven creeks in Idaho and Swan and Big Spring creeks in Utah.

European settlement began in the Bonneville Basin in the mid-1850s to early 1900s (USFWS 2001). By the 1950s, the BCT fishery in Bear Lake was overexploited by commercial and recreational harvest (Behnke and Zarn 1976; Behnke 1992; Lentsch et al. 2000). In addition, land-use disturbances and associated losses in habitat quantity and quality negatively affected the BCT population, particularly in tributaries (Lentsch et al. 2000; Teuscher and Capurso 2007; Williams et al. 2009). Furthermore, Rainbow Trout *O. mykiss* and Lake Trout *Salvelinus namaycush* were introduced into Bear Lake in the early 1900s and likely contributed to the overall decline of BCT in the system (Kershner 1995). The population of BCT in Bear Lake was considered extirpated in the early 1950s (Kershner 1995; Lentsch et al. 2000). In response to the population decline, supplementation of the population with hatchery BCT was deemed necessary (Teuscher and Capurso 2007). Early management of BCT prioritized maintaining and increasing fish yield for harvest; little emphasis was placed on conservation (USFWS 2001). The production of wild BCT in tributaries to Bear Lake was minimal or absent for most years after stocking due to lack of access to suitable spawning habitat (IDFG 2013). However, in the early 2000s, conservation goals shifted towards improving habitat in tributaries to Bear Lake, with the primary goal of increasing production of wild BCT to conserve an important population for ecological and recreational benefits (IDFG 2013). A collaboration between state, federal, and private entities was initiated to construct screens on irrigation diversions to mitigate fish loss, remove or replace culverts that previously functioned as passage barriers, remove or redesign water diversion structures and dams, restore riparian habitat, and ensure stream–lake connectivity after excessive water was diverted for irrigation and power. St. Charles, Fish Haven, and Swan creeks have been the focus of most habitat restoration efforts, and several projects were concluded in the mid-2000s. Since completion of these conservation actions, the composition of hatchery and wild BCT in Bear Lake has changed (Scott Tolentino, UDWR, unpublished data). In the past decade, gill-net surveys, creel surveys, and collections of BCT at the spawning weir on Swan Creek have shown a marked increase in naturally produced BCT. For instance, wild BCT comprised only 5% of the population in the lake in 2002. Despite relatively consistent catch rates for hatchery fish, catch rates of wild BCT increased and wild BCT represented approximately 70% of the population by 2017.

Habitat loss has been a leading factor contributing to the overall decline of salmonids across North America (Williams et al. 1989; Frissell 1993; Horan 2000; Pegg and Chick 2010). Trout abundance has been positively associated with habitat features such as high complexity (Rich et al. 2003), an abundance of large woody debris (Rich et al. 2003), and intact riparian habitat (Horan 2000). Anthropogenic disturbances often reduce the quantity and quality of riparian and instream habitat (Horan 2000; Rich et al. 2003). Habitat complexity is vital to a fish's ability to recover from disturbance, escape predation, obtain necessary food resources, and access important rearing habitat (Horan 2000; Budy et al. 2020). The importance of different habitat characteristics often varies by the age and size of fish. For instance, age-0 Cutthroat Trout occupy stream margins, age-1 fish typically seek low-gradient riffles, and older fish are often found in deep and low-velocity pools (Bisson et al. 1982; Horan 2000; Heckel et al. 2020). However, the ecology and early life history characteristics of BCT in tributaries to Bear Lake are poorly understood. Most data associated with juvenile BCT habitat use are unpublished or anecdotal (e.g., Nielson and Lentsch 1988; Kershner 1995). Habitat relationships for juvenile BCT are thought to be similar to those for other Cutthroat Trout subspecies, but habitat associations for juvenile BCT are poorly documented, particularly for adfluvial populations.

Describing the distribution, abundance, and out-migration characteristics is critical to better understanding adfluvial BCT in the Bear Lake system. As such, the specific objectives of this study were to (1) investigate the distribution and relative abundance of BCT in tributaries to Bear Lake, (2) assess the relationship between habitat characteristics and BCT distribution and abundance, and (3) evaluate characteristics associated with BCT out-migration to Bear Lake. These findings provide insight for natural resource managers to make informed decisions regarding the management of the wild BCT population and fishery.

METHODS

Fish–habitat surveys.— Production of juvenile BCT was evaluated in three tributaries to Bear Lake: St. Charles, Fish Haven, and Swan creeks (Figure 1). Big Spring Creek was excluded from the study due to the presence of an earthen dam about 2 km upstream from Bear Lake that blocks movement of fish in and out of the system. The remaining three tributaries are considered the only systems contributing production to Bear Lake. Although the study tributaries are in relatively close proximity, each stream is quite unique. St. Charles Creek is the largest tributary to Bear Lake (i.e., ~20 km long) and enters the lake on the northwest shoreline. St. Charles Creek splits into two smaller streams (known as the “Big Arm” and “Little Arm”) approximately 3 km from Bear Lake. The main stem of St. Charles Creek flows through forested riparian habitat, with high gradient and stream velocity near its headwaters. The upper portion of the main stem is dominated by large substrate types (i.e., boulders and cobble). The lower portion of the main stem is characterized by moderate gradient and stream velocity, gravel substrate, and riparian habitat composed mostly of willows *Salix* spp. alongside agricultural fields. The Big Arm of St. Charles Creek carries approximately 75% of the main stem’s discharge (U.S. Forest Service, unpublished data). The Big Arm is relatively wide and sinuous and contains high proportions of fine substrate. The Big Arm is further characterized by low gradient, low stream velocity, and little canopy cover. The upper reaches of the Little Arm of St. Charles Creek are dominated by gravel substrate and abundant canopy and instream cover. In its lower reaches, the Little Arm is mostly channelized and is characterized by low gradient and velocity, fine substrate, and abundant aquatic vegetation. Both the Big Arm and Little Arm of St. Charles Creek flow through active agricultural land. Fish Haven Creek originates in an alpine meadow approximately 13 km from the west side of the lake. The upper portion is dominated by fine substrate and low gradient. The middle portion of Fish Haven Creek is characterized by forested habitat, high gradient, large substrates, and relatively cold water temperatures. The lower portion of Fish Haven Creek is dominated by gravel substrate, high proportions of canopy cover, and moderate gradient and stream velocity. Swan Creek originates from a large mountainside spring approximately 3 km from Bear Lake just south of the Idaho–Utah border. Swan Creek is characterized by high gradient and stream velocity in its upper reaches that become more moderate in downstream reaches. Lower reaches in both Fish Haven and Swan creeks flow through private properties that do not employ agricultural practices. The riparian habitat in these reaches is dominated by willows and other deciduous woody vegetation.

A systematic sampling design was used to select sample reaches in each tributary. In total, 75 reaches were sampled in 2019 and 2020. Sampling occurred on the descending limb of the hydrograph and when BCT spawning had mostly concluded (Curry et al. 2009; Meyer et al. 2010; Sindt et al. 2012). Due to high flows in 2019, sampling began later in the summer (late June) than originally planned. In 2020, the summer sampling season began during the second week of June. The length of each reach was 35 times the mean wetted stream width, with a maximum length of 300 m. Stream reaches were further subdivided into individual macrohabitats (i.e., pool, riffle, run; Sindt et al. 2012). Each reach was georeferenced using a GPS and marked with surveyor’s tape. Due to logistical issues (e.g., lack of landowner permission and boat access), several systematically selected sites were omitted from the Big Arm of St. Charles Creek.

Fish were sampled in each reach using a battery-powered backpack electrofishing unit (Model LR-24; Smith-Root, Inc., Vancouver, Washington). A backpack electrofishing team consisted of one person with the electrofishing unit, followed by two netters using dip nets with 6-mm delta mesh. When water velocity and depth allowed, block nets were placed at the upper and lower ends of each reach; otherwise, reaches terminated at a transition between macrohabitats (Meyer and High 2011). Due to

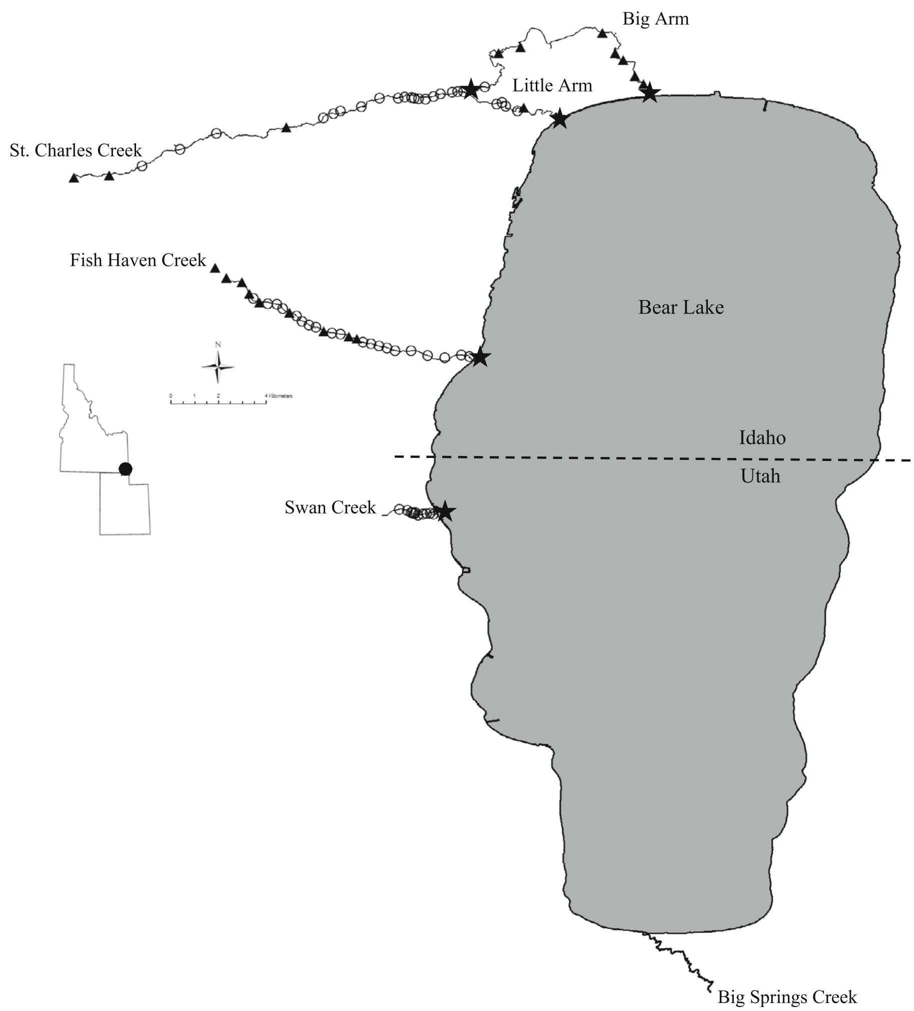

FIGURE 1. Tributary sites where habitat assessments and electrofishing surveys were conducted during 2019 and 2020 in three tributaries to Bear Lake, Idaho–Utah. Stream sites where Bonneville Cutthroat Trout (BCT) were present are symbolized by hollow circles, and sites where BCT were absent are symbolized by black triangles. Passive integrated transponder tag antennas are symbolized by black stars. The approximate location of the study area in Idaho and Utah is represented by a black oval in the inset.

depth constraints in five reaches on the Big Arm of St. Charles Creek, a generator-powered electrofishing unit (Infinity model; Midwest Lake Electrofishing, Polo, Missouri) was used in conjunction with a drift boat. Prior to sampling, water temperature (°C) and conductivity (μS/cm) were measured in each reach using a handheld thermometer and probe (DiST; Hanna Instruments, Woonsocket, Rhode Island). Sampling began with 30-Hz pulsed DC, 12% duty cycle, and 100 V. If these settings were ineffective at eliciting a response (i.e., tetany), voltage output, pulse width, and frequency (Hz) were adjusted accordingly (Dunham et al. 2009). Electrofishing proceeded in an upstream direction. An effort was made to sample all available habitat in each reach. Seconds of electrofishing (i.e., effort) were recorded as the time when electricity was applied to the water.

Sampled fish were identified, and TL was measured to the nearest millimeter. Hybridization between Rainbow Trout and Cutthroat Trout has been documented in St. Charles Creek (Campbell et al. 2007). Although we did not collect tissue samples for genetic analysis, Rainbow Trout × Cutthroat Trout hybrids (hereafter, referred to as "hybrids") were identified as having phenotypic traits similar to those of BCT but possessing white leading tips on the anal and pelvic fins and lacking a bright-red-orange throat slash (Meyer et al. 2017). From all sampled BCT, scales were removed from the area posterior to the dorsal fin and dorsal to the lateral line. Scales were placed in coin envelopes and transported to the laboratory for processing. To evaluate out-migration, all BCT longer than 70 mm were tagged in the abdominal cavity with 12-mm half-duplex (HDX) PIT tags (Oregon RFID, Portland, Oregon) following standard methodology (Achord et al. 1996; Bateman et al. 2009). Previous research suggests that juvenile salmonids have PIT tag retention rates over 90% (Meyer and High 2011; Ostrand et al. 2012; Foldvik and Kvingedal 2018). In addition to stream surveys that included habitat assessments, electrofishing surveys were conducted in other sections (i.e., not part of the systematic sample) of stream in an effort to increase sample size of tagged BCT; all fish sampled during these surveys were excluded from the evaluation of habitat relationships. All age-0 BCT (≤60 mm) were removed from analyses due to the inherent size selectivity of electrofishing and inconsistencies in sampling smaller fish (Reynolds and Kolz 2012; Budy et al. 2020).

Large-scale habitat characteristics (elevation [m], gradient [%], and distance to Bear Lake [km]) were estimated using ArcMap (ESRI, Redlands, California) and Google Earth (Google, Mountain View, California). Gradient was calculated as the distance between contour lines that encompassed the sampling reach divided by the length of the reach (Meyer et al. 2003). Small-scale habitat characteristics were quantified in each reach immediately after fish sampling. Habitat was measured separately for each macrohabitat unit (Sindt et al. 2012; Heckel et al. 2020). Macrohabitat length was measured along the thalweg. Transects were established at 25, 50, and 75% of the macrohabitat unit length if the macrohabitat was ≥30 m and at 25% and 75% if the macrohabitat was ≤30 m. Depth (m), velocity (m/s), substrate composition (%), and substrate embeddedness (%) were measured along the transects at 20, 40, 50, 60, and 80% of the wetted width. Depth was measured to the nearest 0.1 m using a top-set wading rod. Benthic and mean current velocity were measured. Benthic current velocity was measured at 0.03 m above the substrate. Mean current velocity was measured at 60% of the total depth using a portable velocity meter (Flo-Mate Model 2000; Marsh-McBirney, Inc., Loveland, Colorado) if depth of the water column was less than 1 m. If depth exceeded 1 m, measurements were taken at 20% and 80% of the water column and a mean was used to estimate current velocity (Flotemersch et al. 2001; Sindt et al. 2012; Heckel et al. 2020). Dominant substrate composition was classified using a modified Wentworth scale as follows: silt and sand (<2 mm in diameter), gravel (2–64 mm), cobble (65–256 mm), boulder (>256 mm), or bedrock (Wentworth 1922; Cummins 1962; Sindt et al. 2012). Embeddedness was visually estimated to the nearest 25% (i.e., 25, 50, 75, or 100%) for gravel, cobble, and boulder substrates at each macrohabitat transect point (McHugh and Budy 2005).

To characterize thermal regime, a temperature logger (Onset HOBO Data Logger; Onset Computer Corporation, Bourne, Massachusetts) was deployed at each stationary antenna (see antenna description below) as well as in the headwaters, at the midpoint, and at the mouth of each stream. Temperature loggers were deployed at the beginning of each field season and removed when stream surveys were concluded. Each temperature logger recorded hourly water temperature for the duration of the time it was deployed.

Instream cover (m^2) was classified as boulders, aquatic macrophytes, roots, overhanging vegetation, undercut bank, and large wood. One length measurement, three width measurements, and three depth measurements were recorded for all cover that was at least 0.3 m in length, in water at least 0.2 m deep, and occurred 2 m downstream or upstream of each transect (Quist et al. 2003; Sindt et al. 2012). Canopy cover (%) was measured at each transect using a spherical concave densiometer facing each streambank and facing upstream and downstream at the midpoint of the stream channel. Bank characteristics were visually estimated along each transect on both sides (i.e., woody vegetation, nonwoody vegetation, boulders, eroded ground, bare ground; Quist et al. 2003; Sindt et al. 2012).

The area of each macrohabitat within a stream reach was estimated by multiplying the mean wetted width of all transects by the thalweg length. Means were calculated for wetted width, depth, velocity, substrate embeddedness, canopy cover, and daily temperature for each macrohabitat. Additionally, the proportion of different substrates, bank characteristics, and instream cover type (i.e., nonwoody and woody) were calculated separately for each macrohabitat. Habitat characteristics were averaged across macrohabitats in a stream reach. Habitat characteristics were then weighted by the proportion of the reach area that was represented by each macrohabitat. Weighted values were summed to quantify habitat characteristics for the entire stream reach. In addition, mean CVs of velocity, canopy cover, depth, and width were calculated ($CV = 100 \times SD/mean$) to provide an index of habitat complexity and heterogeneity.

Additional habitat variables were created by combining two or more variables. The proportions of cobble and boulder substrate were combined to create a large-substrate variable. The areas (m^2) of different cover types were combined to form a total instream cover variable. Additional variables that were hypothesized to predict the probability of PIT-tagged BCT out-migrating to Bear Lake were also created (e.g., age and length of tagged fish; number of downstream diversions).

Scales from sampled BCT were placed between two glass slides and then viewed under a microscope using transmitted light. Scales were further evaluated with an image analysis system (Image-Pro Plus, Media Cybernetics, Rockville, Maryland). A single experienced reader estimated ages and measured distance between annuli for all fish using standard methodologies for annulus identification (McInerny 2017). High frequencies of "retarded" scale formation were observed in BCT across all three tributaries; therefore, first-year annuli were missing in a relatively high proportion of fish. The formation of scales in the first year has been related to growth rate for Yellowstone Cutthroat Trout *O. clarkii bouvieri* in Yellowstone Lake, Wyoming (Laakso and Cope 1956). Lentsch and Griffith (1987) hypothesized that squamation in salmonids is frequently delayed in high-elevation systems with short growing seasons. Therefore, age was increased by 1 year when BCT had more than six circuli before the formation of a first annulus (Laakso and Cope 1956).

To monitor out-migration of PIT-tagged BCT, stationary HDX PIT antennas were installed near the terminus of each of the three study tributaries. An antenna was installed upstream of the fork on St. Charles Creek, and additional antennas were constructed near the mouth of the Big and Little arms. We sought to place antennas as close as possible to Bear Lake, but landowner permission and stream channel characteristics dictated final locations. The antenna on the Big Arm of St. Charles Creek was located 36 m upstream of Bear Lake, and the antenna on the Little Arm was located 340 m from Bear Lake. The antenna on Fish Haven Creek was located 200 m from the mouth of the creek, and the antenna on Swan Creek was located 82 m from the mouth. Because of the proximity to Bear Lake, fish detected at antennas located near the mouth of each stream were assumed to have successfully out-migrated to Bear Lake. Each HDX antenna consisted of a 142-L cooler (Grizzly, Decorah, Iowa), two to four 12-V batteries (connected in parallel; Sun Xtender Solar Batteries, West Covina, California), and one HDX PIT tag data logger (Oregon RFID). Each antenna station had one or two 140-W solar panels (Solartech Power, Inc., Ontario, California) to charge batteries and help power the system. Twinaxial cable connected the data logger to an antenna-tuning box. A pass-through design was constructed for each antenna, with a loop of wire passing around the stream and connecting to the antenna-tuning box. However, a pass-over design was implemented for the months of August–October on the main stem of St. Charles Creek in 2019 to prevent newly introduced cattle from damaging the antenna wire. Polypropylene rope was stretched above the stream and was secured to the top of the antenna wire for additional support for all pass-through antennas.

The arrays were operational from June to October in 2019 and from May to October in 2020. Beginning in mid-July to early August 2020, the antenna on Swan Creek worked intermittently due to technical issues, but the issues were resolved on August 9, 2020. The efficiency of each antenna was evaluated using monthly detection tests. A PIT tag was inserted into a plastic fish and passed through each antenna 10 times, with parallel and perpendicular orientations to the antenna (Zydlewski et al. 2006). Efficiency estimates were consistently 100%.

Data analysis.— Spearman's rank correlation coefficient (r_s) was used to investigate multicollinearity among habitat characteristics (Meyer et al. 2010; Sindt et al. 2012; Smith et al. 2016). Habitat variables with r_s values $\geq |0.70|$ were considered highly correlated, and only the most ecologically relevant variable was retained in candidate models (Meyer et al. 2010; Sindt et al. 2012). For example, total instream cover was highly correlated with the proportion of other cover types. Total cover was deemed the most ecologically relevant variable; therefore, total cover was retained in candidate models.

Differences in length and age structure among streams were evaluated using a Kruskal–Wallis test, followed by pairwise Wilcoxon rank-sum tests (Higgins 2004). A type-I error rate of 0.05 was used for statistical tests. Catch per unit effort (CPUE = fish/min of electrofishing) of BCT was standardized to 100 m of stream length (Meyer et al. 2006). Relative abundance and occurrence of BCT were evaluated using a hurdle regression modeling technique consisting of two submodels (Wenger and Freeman 2008; Meyer et al. 2010; Smith et al. 2016). Two-stage hurdle models allow for the hypothesis that factors predicting fish occurrence and relative abundance are not always the same (Wenger and Freeman 2008). The submodel evaluating occurrence of BCT used logistic regression to assess the occurrence of BCT across all reaches. The other submodel evaluating relative abundance used a Poisson distribution for sample reaches where at least one BCT was present (Martin et al. 2005). Additionally, analyses for occurrence and relative abundance were conducted at multiple spatial scales (i.e., large and small scales). The probability of out-migration of BCT in the study streams was investigated by using logistic regression.

Models were constructed using the GLM (generalized linear model) function in program R (R Core Team 2020). The dispersion parameter ($\hat{c}$) was calculated as the Pearson's residual deviance divided by the residual degrees of freedom. Models were considered overdispersed if $\hat{c} \geq 1$ (Burnham and Anderson 2002). A $\hat{c}$ greater than 1 indicated that the model did not fit the data well or the data were overdispersed (Burnham and Anderson 2002). McFadden's pseudo-R^2 was used as an indication of model fit and was calculated as 1 minus the difference in the log likelihood of a model with parameters and the intercept-only model (McFadden 1974). McFadden's pseudo-R^2 values of 0.20–0.40 indicate excellent model fit; however, models with values as low as 0.10 have also been shown to have good fit (McFadden 1974; Hosmer and Lemeshow 1989). Models predicting occurrence and relative abundance of BCT included 3 large-scale variables and 18 small-scale variables (Table 1). Models predicting the probability of out-migration of BCT included 22

TABLE 1. Mean and SE (in parentheses) of abiotic and biotic variables measured from 75 reaches in three tributaries to Bear Lake, Idaho–Utah, during 2019 and 2020. Large- and small-scale variables were used as independent variables in candidate models of occurrence, relative abundance, and probability of out-migration of Bonneville Cutthroat Trout (BCT). Out-migration variables were used in candidate models of probability of BCT out-migration only.

		St. Charles Creek				
Variable	Description	Main stem	Little Arm	Big Arm	Fish Haven Creek	Swan Creek
		Large-scale variables				
Elevation	Elevation (m) of the upstream end of the stream reach	1,883.09 (17.3)	1,813.40 (0.87)	1,810.5 (1.10)	2,012.35 (23.11)	1,825.00 (2.85)
Gradient	Reach length divided by the elevation change (%)	2.17 (0.36)	0.70 (0.12)	0.24 (0.07)	5.70 (0.79)	2.19 (0.28)
Distance to lake	Distance (m) of the upstream end of the reach to lake	8,255.55 (695.99)	2,016.00 (188.48)	3,950.13 (1,113.72)	4,522.70 (441.36)	647.00 (92.60)
		Small-scale variables				
Reach area	Total area of stream reach (m^2)	1,148.33 (114.00)	1,079.98 (228.52)	6,271.19 (1,395.04)	447.80 (39.0)	984.30 (137.60)
Temperature	Mean daily stream temperature during sampling period	9.03 (0.32)	13.34 (1.28)	18.24 (1.60)	7.68 (0.25)	8.95 (0.22)
Runs	Proportion of reach area as run	0.40 (0.09)	0.52 (0.20)	0.96 (0.05)	0.10 (0.05)	0.04 (0.04)
Pool depth	Mean depth of pool(s)	0.35 (0.06)	0.35 (0.15)	0.08 (0.07)	0.06 (0.02)	0.19 (0.08)
Depth	Mean water depth (m)	0.43 (0.01)	0.43 (0.02)	0.71 (0.08)	0.20 (0.01)	0.34 (0.03)
$Depth_{CV}$	Mean CV of depth	39.28 (2.08)	46.38 (5.36)	25.56 (3.70)	41.80 (1.90)	46.90 (4.00)
Width	Mean stream width (m)	7.03 (0.62)	6.58 (0.23)	20.23 (4.63)	3.54 (0.26)	6.24 (0.47)
$Width_{CV}$	Mean CV of stream width	14.66 (1.71)	13.92 (2.49)	18.45 (4.01)	29.40 (3.07)	22.90 (3.00)
Velocity	Mean current velocity (m/s)	0.41 (0.03)	0.14 (0.07)	0.08 (0.05)	0.38 (0.03)	0.37 (0.07)
Canopy cover	Mean canopy cover (%)	45.23 (3.78)	25.87 (5.53)	8.45 (7.72)	62.60 (4.50)	66.72 (6.20)
Canopy $cover_{CV}$	Mean CV of canopy cover	86.83 (10.3)	115.43 (28.87)	65.45 (35.55)	48.20 (7.40)	44.20 (5.50)
Fine substrate	Proportion of silt and sand substrate	0.11 (0.02)	0.53 (0.20)	0.88 (0.13)	0.13 (0.04)	0.06 (0.03)
Gravel substrate	Proportion of gravel substrate	0.38 (0.06)	0.47 (0.20)	0.09 (0.08)	0.37 (0.03)	0.29 (0.06)
Large substrate	Proportion of cobble and boulder substrate	0.39 (0.07)	0.00 (0.00)	0.04 (0.04)	0.48 (0.04)	0.56 (0.08)
Embeddedness	Proportion of substrate that is covered in silt and sand	34.84 (2.16)	21.52 (8.69)	5.63 (4.63)	37.41 (2.27)	36.60 (3.00)
Cover area	Mean sum of the area of instream cover in transects (m^2)	23.65 (5.87)	24.00 (11.94)	41.34 (11.22)	1.6 (0.71)	30.60 (10.90)
Proportion NWC	Proportion of transect with non-woody cover	0.15 (0.06)	0.05 (0.02)	0.09 (0.03)	0.01 (0.01)	0.07 (0.02)
BKT CPUE	Brook Trout CPUE in reaches	0.23 (0.05)	1.22 (0.48)	0.11 (0.11)	–	–
Length	TL (mm) of BCT	127.16 (4.16)	118.56 (3.57)	124.39 (5.93)	128.72 (2.78)	129.10 (3.62)
Age	Age (years) of BCT	1.43 (0.06)	1.27 (0.06)	1.48 (0.11)	1.36 (0.04)	1.52 (0.06)
Diversions	Number of downstream diversions	5.92 (0.07)	1.83 (0.04)	3.00 (0.00)	2.34 (0.08)	0.18 (0.02)

abiotic and biotic variables, and probability of out-migration was evaluated with 30 candidate models. Eight candidate models created a priori were used to evaluate the relationship of BCT occurrence and relative abundance as a function of large-scale habitat characteristics for each submodel. Small-scale habitat characteristics were investigated with 30–35 candidate models for each submodel.

All models for occurrence, relative abundance, and probability of out-migration were investigated separately by tributary. All competing regression models that were not overdispersed were ranked using Akaike's information criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). If models were overdispersed ($\hat{c} > 1$), quasi-AIC_c ($QAIC_c$) was used to rank candidate models and an additional parameter was added to the number of parameters K. All models within 2 AIC_c or $QAIC_c$ units of the best model were retained as top models. Furthermore, the sum of Akaike weights (w) for each variable retained in top models was used to highlight the importance of independent variables for the occurrence and relative abundance of BCT (Burnham and Anderson 2002; Quist and Hubert 2005; Meyer and High 2011).

RESULTS

In St. Charles Creek, 1,833 individual fish representing 11 different species were sampled, including 406 BCT. In Swan Creek, 292 BCT and 4 hybrids were sampled. Bonneville Cutthroat Trout was the only fish species sampled in Fish Haven Creek ($n = 368$). Bonneville Cutthroat Trout occurred in 24 of 35 (68.6%) reaches in St. Charles Creek, 20 of 29 (68.9%) reaches in Fish Haven Creek, and all reaches in Swan Creek. Although BCT were relatively common in St. Charles Creek, occurrence of BCT was highly variable when compared across the three sections (main stem, Big Arm, and Little Arm). Bonneville Cutthroat Trout occurred at 86% of the reaches on the main stem, 13% of reaches on the Big Arm, and 80% of reaches on the Little Arm (Figure 1). Brook Trout *Salvelinus fontinalis* only occurred in St. Charles Creek and were present in 66% of reaches. Probable hybrids were sampled at 31% of sites on St. Charles Creek and 9% of sites on Swan Creek.

Total lengths of fish were significantly different across streams ($P < 0.05$). Length structure was similar for BCT in Fish Haven and Swan creeks ($P \geq 0.05$) and larger than fish in St. Charles Creek ($P < 0.05$). Bonneville Cutthroat Trout in St. Charles Creek were approximately 16% smaller (median ± SE = 105 ± 3.0 mm) than those in Fish Haven Creek (115 ± 3.9 mm) and Swan Creek (111 ± 4.2 mm; Figure 2). Catch rates were highest in Swan Creek (mean ± SE = 0.67 ± 0.11 fish/min), followed by St. Charles Creek (0.19 ± 0.03 fish/min) and Fish Haven Creek (0.16 ± 0.04 fish/min). Estimated ages from 595 BCT varied from 1 to 6 years in St. Charles Creek, 1 to 7 years in Fish Haven Creek, and 1 to 5 years in Swan Creek (Figure 2). Age structure was similar among streams ($P \geq 0.05$; Figure 3).

Abiotic and biotic characteristics were highly variable among the three tributaries (Table 1). Regression models suggested that habitat characteristics related to BCT occurrence differed from those associated with relative abundance (Table 2). Logistic regression models indicated that the presence of BCT in St. Charles Creek was positively associated with distance to Bear Lake, gradient, CV of depth, canopy cover, and total cover. Elevation and stream width were negatively associated with the occurrence of BCT in St. Charles Creek. In Fish Haven Creek, the presence of BCT was positively associated with stream temperature, instream cover area, and CV of velocity but negatively associated with elevation, distance to Bear Lake, and the proportion of fine substrate (i.e., silt, sand). Models were not developed for occurrence of BCT in Swan Creek because BCT were present in all reaches. Relative abundance of BCT in St. Charles Creek increased with CV of canopy cover and decreased with stream width and canopy cover (Tables 2, 3). The relative abundance of BCT in Fish Haven Creek was negatively related to elevation, channel gradient, and distance to Bear Lake. In Swan Creek, the relative abundance of BCT was negatively associated with elevation, distance to Bear Lake, channel gradient, and stream velocity.

In St. Charles Creek, 307 BCT were PIT-tagged (mean length ± SE = 128 ± 3.1 mm); 311 BCT in Fish Haven Creek (137 ± 4.0 mm) and 251 BCT in Swan Creek (135 ± 4.1 mm) were PIT-tagged. Of these fish, 214 (25%) were detected at stationary antennas during out-migration from the three tributaries. The proportion of BCT that out-migrated from St. Charles Creek (5.5%) was lower than proportions for Fish Haven Creek (50.2%) and Swan Creek (16.3%). In general, the mean length of out-migrating BCT was 25% greater than the mean length of all BCT that were PIT-tagged, suggesting that large PIT-tagged BCT were more likely to out-migrate than smaller fish (Figure 4). Average length of BCT out-migrating in Swan Creek was the largest among the three tributaries (184 ± 4.1 mm), followed by St. Charles Creek (170 ± 2.4 mm) and Fish Haven Creek (148 ± 3.7 mm). Ages of tagged BCT varied from 1 to 6 years in St. Charles Creek, 1 to 7 years in Fish Haven Creek, and 1 to 5 years in Swan Creek. All ages of tagged BCT were detected out-migrating in both St. Charles and Fish Haven creeks, but we did not detect any tagged age-5 fish out-migrating in Swan Creek. Age-1 BCT were the most frequently tagged in all three tributaries and were the most common to out-migrate in Fish Haven Creek. Interestingly, age-2 BCT were the most common to out-migrate in St. Charles and

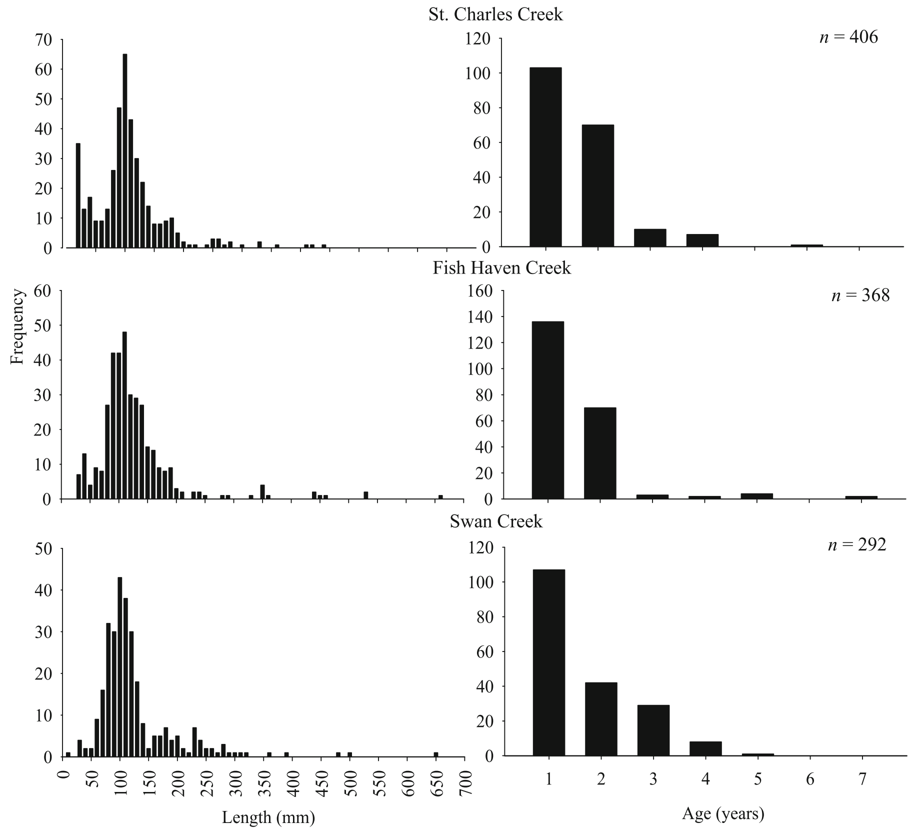

FIGURE 2. Length- and age-frequency distributions of Bonneville Cutthroat Trout sampled in tributaries to Bear Lake, Idaho–Utah, during 2019 and 2020.

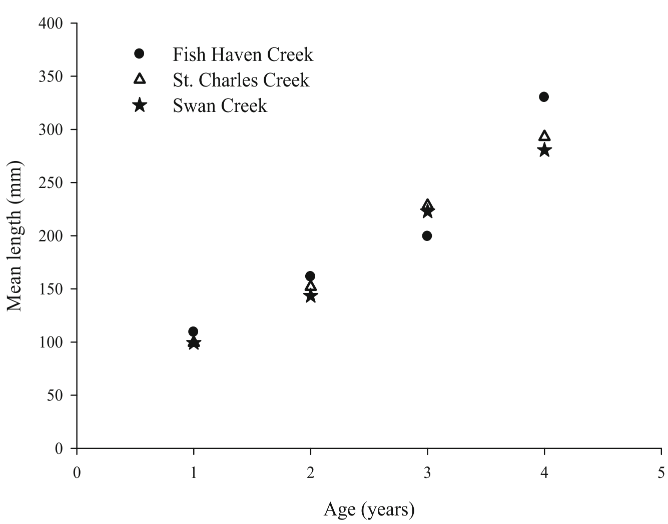

FIGURE 3. Mean length at age at time of capture for Bonneville Cutthroat Trout sampled in tributaries to Bear Lake, Idaho–Utah, during 2019 and 2020.

Swan creeks (Figure 4). The dates of out-migration for BCT in St. Charles and Fish Haven creeks were the most widely distributed, with detections beginning in early May and ending in early October. The range of out-migration dates in Swan Creek was narrower, with out-migration beginning in late June and ending in early October. The peak of BCT out-migration occurred in August in all three study streams (Figure 5).

Abiotic and biotic factors related to the probability of BCT out-migration varied between the three tributaries. The probability that a fish out-migrated was positively associated with fish length for St. Charles and Fish Haven creeks (Table 4). The probability that fish out-migrated was negatively associated with distance to Bear Lake for St. Charles Creek and the number of downstream irrigation diversions (i.e., from site of tagging) for Fish Haven Creek. In Swan Creek, the probability of out-migration of BCT was positively associated with fish age and negatively associated with distance to Bear Lake (Table 4).

DISCUSSION

Persistence of fishes is largely influenced by the presence, abundance, and spatial distribution of suitable habitat; thus, identification of abiotic and biotic factors that may limit species distribution is vital for effective conservation (Kruse et al. 1997; Rich et al. 2003; Ertel et al.

TABLE 2. The top logistic regression models investigating the presence–absence and relative abundance of Bonneville Cutthroat Trout among stream reaches ($n = 75$) sampled during 2019 and 2020. Akaike's information criterion adjusted for small sample size (AIC_c) or quasi-AIC_c ($QAIC_c$) was used to rank the candidate models. Only candidate models within 2.00 AIC_c or $QAIC_c$ units of top model were retained. Delta AIC_c (ΔAIC_c) or delta $QAIC_c$ ($\Delta QAIC_c$), total number of parameters (K), model weight (w_i), and McFadden's pseudo-R^2 are included. Direction of effect for each covariate is indicated (positive [+] or negative [−]).

Stream	Response variable	Model parameters	AIC_c or $QAIC_c$	ΔAIC_c or $\Delta QAIC_c$	K	w_i	R^2
		Large-scale models					
St. Charles Creek	Presence–absence	+ Distance to lake − Elevation	45.7	0.00	3	0.22	0.11
		+ Distance to lake + Gradient − Elevation	45.9	0.24	4	0.20	0.16
		+ Gradient	47.6	1.90	2	0.09	0.01
		+ Distance to lake	47.6	1.92	2	0.09	0.01
		Small-scale models					
		+ $Depth_{CV}$ + Canopy cover + Cover area	25.5	0.00	4	0.31	0.63
		+ $Depth_{CV}$ + Canopy cover	26.4	0.92	3	0.19	0.55
		+ $Depth_{CV}$ − Width + Cover area	26.7	1.23	4	0.17	0.60
		+ $Depth_{CV}$ − Width	27.0	1.57	3	0.14	0.53
		+ $Depth_{CV}$	27.4	1.94	2	0.12	0.47
St. Charles Creek	Relative abundance	**Large-scale models**					
		Null model	46.9	0.00	2	0.34	0.00
		Small-scale models					
		− Width − Canopy cover	112.2	0.00	4	0.53	0.15
		− Width + Canopy $cover_{CV}$	114.0	1.74	4	0.22	0.14
Fish Haven Creek	Presence–absence	**Large-scale models**					
		− Elevation	30.7	0.00	2	0.42	0.27
		− Distance to lake	31.6	0.94	2	0.26	0.24
		Small-scale models					
		+ Cover area − Fine substrate	29.4	0.00	3	0.34	0.38
		+ $Velocity_{CV}$ + Temperature − Fine substrate	30.1	0.71	4	0.24	0.43
		+ Cover area + Temperature − Fine substrate	30.8	1.38	4	0.17	0.41
Fish Haven Creek	Relative abundance	**Large-scale models**					
		− Distance to lake	47.5	0.00	3	0.38	0.27
		− Elevation	48.0	0.55	3	0.29	0.26
		− Distance to lake − Gradient	48.9	1.37	4	0.19	0.28
		− Elevation − Gradient	49.5	1.97	4	0.14	0.27
		Small-scale models					
		Null model	44.7	0.00	3	0.12	0.00
Swan Creek	Relative abundance	**Large-scale models**					
		− Elevation	27.4	0.00	3	0.46	0.23
		− Elevation − Gradient	29.2	1.79	4	0.19	0.24
		− Distance to lake	29.4	1.96	3	0.17	0.16
		Small-scale models					
		− Velocity	32.7	0.00	3	0.64	0.29

2017). Previous studies quantifying the ecology and habitat characteristics of BCT are underrepresented in the literature (Kershner 1995; Budy et al. 2012). However, studies have been conducted to assess habitat relations of other subspecies of Cutthroat Trout that may provide insight on the habitat requirements of BCT. Previous

TABLE 3. Sum of Akaike weights (*w*), direction of relationship (positive or negative), parameter estimates, and SE for each independent variable in top logistic regression models investigating presence–absence, relative abundance, and probability of out-migration of Bonneville Cutthroat Trout among stream reaches ($n = 75$) sampled during 2019 and 2020.

Stream	Independent variable	*w*	Parameter estimate	SE
		Presence–absence		
St. Charles Creek	Depth_{CV}	(+) 0.93	0.26	0.11
	Distance to lake	(+) 0.51	0.00	0.00
	Canopy cover	(+) 0.50	0.06	0.04
	Cover area	(+) 0.48	0.05	0.04
	Elevation	(−) 0.42	−0.02	0.02
	Width	(−) 0.31	−0.07	0.01
	Gradient	(+) 0.29	0.25	0.42
Fish Haven Creek	Fine substrate	(−) 0.75	−1.19	1.30
	Cover area	(+) 0.51	0.55	0.72
	Elevation	(−) 0.42	−0.01	0.01
	Temperature	(+) 0.41	0.33	0.52
	Distance to lake	(−) 0.26	−0.00	0.00
	$\text{Velocity}_{\text{CV}}$	(+) 0.24	0.01	0.02
		Relative abundance		
St. Charles Creek	Width	(−) 0.75	−0.12	0.04
	$\text{Canopy cover}_{\text{CV}}$	(+) 0.22	0.01	0.00
	Canopy cover	(−) 0.22	−0.01	0.00
Fish Haven Creek	Distance to lake	(−) 0.57	−0.00	0.00
	Elevation	(−) 0.43	−0.01	0.00
	Gradient	(−) 0.33	−0.07	0.05
Swan Creek	Elevation	(−) 0.65	−0.05	0.01
	Velocity	(−) 0.64	−1.62	0.26
	Gradient	(−) 0.19	−0.01	0.21
	Distance to lake	(−) 0.17	−0.00	0.00
		Probability of out-migration		
St. Charles Creek	Length	(+) 0.80	0.02	0.00
	Distance to lake	(−) 0.80	−0.00	0.00
Fish Haven Creek	Length	(+) 0.74	0.01	0.00
	Diversions	(−) 0.74	−0.82	0.11
Swan Creek	Age	(+) 0.62	1.17	0.22
	Distance to lake	(−) 0.62	−2.88	0.89

research indicated that large-scale abiotic factors, such as gradient, elevation, and stream size, were associated with the occurrence of Yellowstone Cutthroat Trout in northwestern Wyoming (Kruse et al. 1997) and Westslope Cutthroat Trout *O. clarkii lewisi* in northern Idaho (Heckel et al. 2020). In the current study, elevation was an important variable that was negatively associated with occurrence and relative abundance of BCT across all three tributaries. In general, high-elevation reaches were dominated by homogeneous habitat and mid- to low-elevation reaches were composed of complex habitat types. Kruse et al. (2000) found that Yellowstone Cutthroat Trout occurred mostly at lower-elevation sites in headwater streams in Wyoming. Greater abundances of Cutthroat Trout, including BCT, may be supported in downstream reaches because low-elevation stream reaches are often highly productive (Berger and Gresswell 2009).

Heterogeneity in habitat characteristics was important for predicting the occurrence and abundance of BCT in tributaries to Bear Lake. The amount of cover and the CV of several habitat variables were interpreted as indicators of habitat complexity. Previous studies suggest that habitat complexity and heterogeneity positively influence Cutthroat Trout occurrence and abundance (Harvey et al. 1999; Rosenfeld et al. 2000; Berger and Gresswell 2009; Smith et al. 2016). Bonneville Cutthroat Trout were generally absent from reaches with little habitat complexity. Reaches with homogeneous habitat (i.e., low habitat complexity) were often dominated by fine substrate and rarely contained BCT. Similar results have been reported for

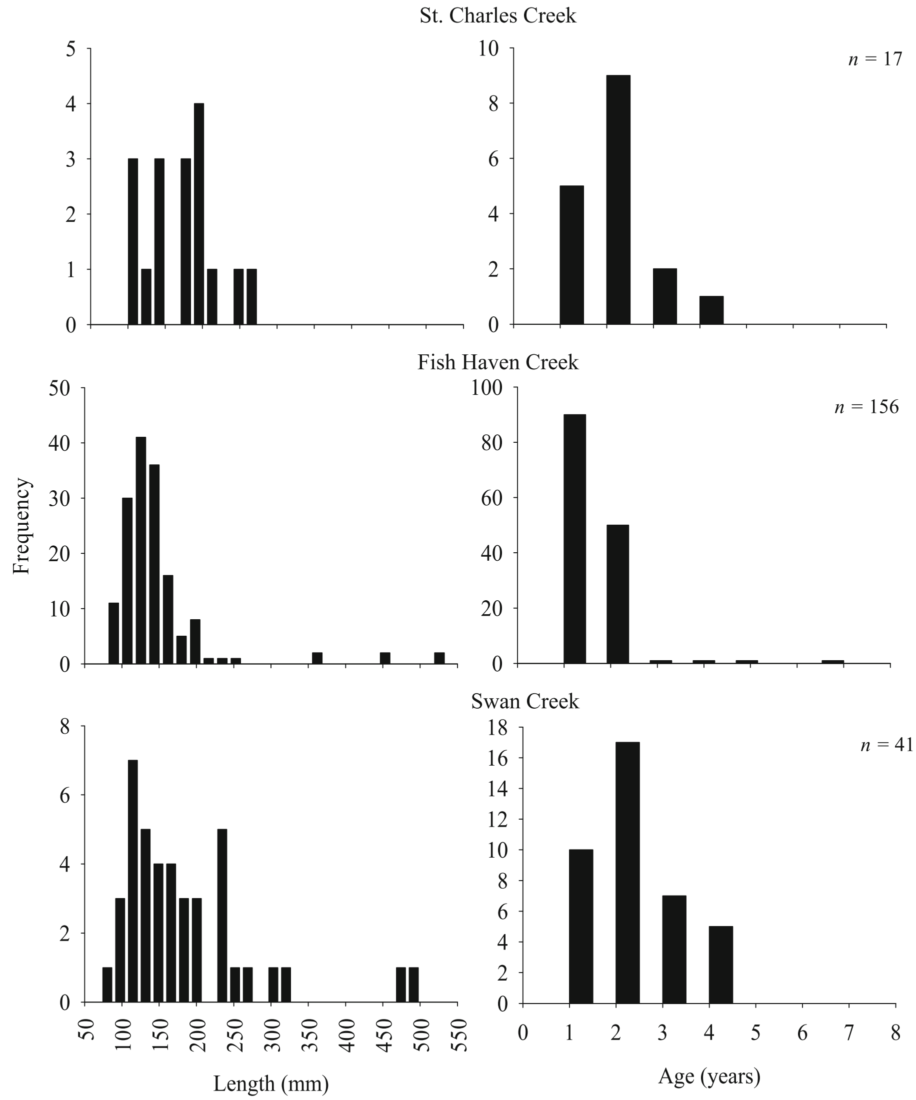

FIGURE 4. Length- and age-frequency distributions of PIT-tagged Bonneville Cutthroat Trout detected out-migrating at stationary antennas located at the mouth of three tributaries to Bear Lake, Idaho–Utah, during 2019 and 2020.

other Cutthroat Trout populations. For example, Budy et al. (2012) found that small increases in sedimentation had significant detrimental effects on survival of juvenile BCT in tributaries of the Logan River, Utah. Additionally, fine substrate composition was inversely related to juvenile Cutthroat Trout abundance in a coastal stream in British Columbia (Rosenfeld et al. 2000) and the occurrence of Westslope Cutthroat Trout in tributaries to the St. Maries River, Idaho (Heckel et al. 2020).

Additional small-scale variables influenced the occurrence and abundance of BCT in tributaries to Bear Lake. For instance, canopy cover was an important variable predicting the occurrence of BCT in tributaries. Canopy cover is critical for providing refuge from overhead predators and for regulating stream temperature (Penaluna et al. 2016; Heckel et al. 2020). Furthermore, sample reaches that had high proportions of canopy cover often had high amounts of wood. Instream woody cover has been positively associated with Cutthroat Trout, likely due to decreased risk of predation and increased habitat complexity (Gowan and Fausch 1996; Harvey et al. 1999; Berger and Gresswell 2009; Young 2011). In this study, instream cover was positively related to the presence of BCT in the study streams. Specifically, the area of instream woody cover was 1.6 times greater than the area of nonwoody cover in sites where BCT were present. This pattern suggests that all instream cover is important, but woody cover may be most important to BCT. Stream width was also an important factor in models assessing the occurrence and abundance of BCT. Rosenfeld et al. (2000) found that stream width had a negative relationship with presence of juvenile Cutthroat Trout, and fish were often

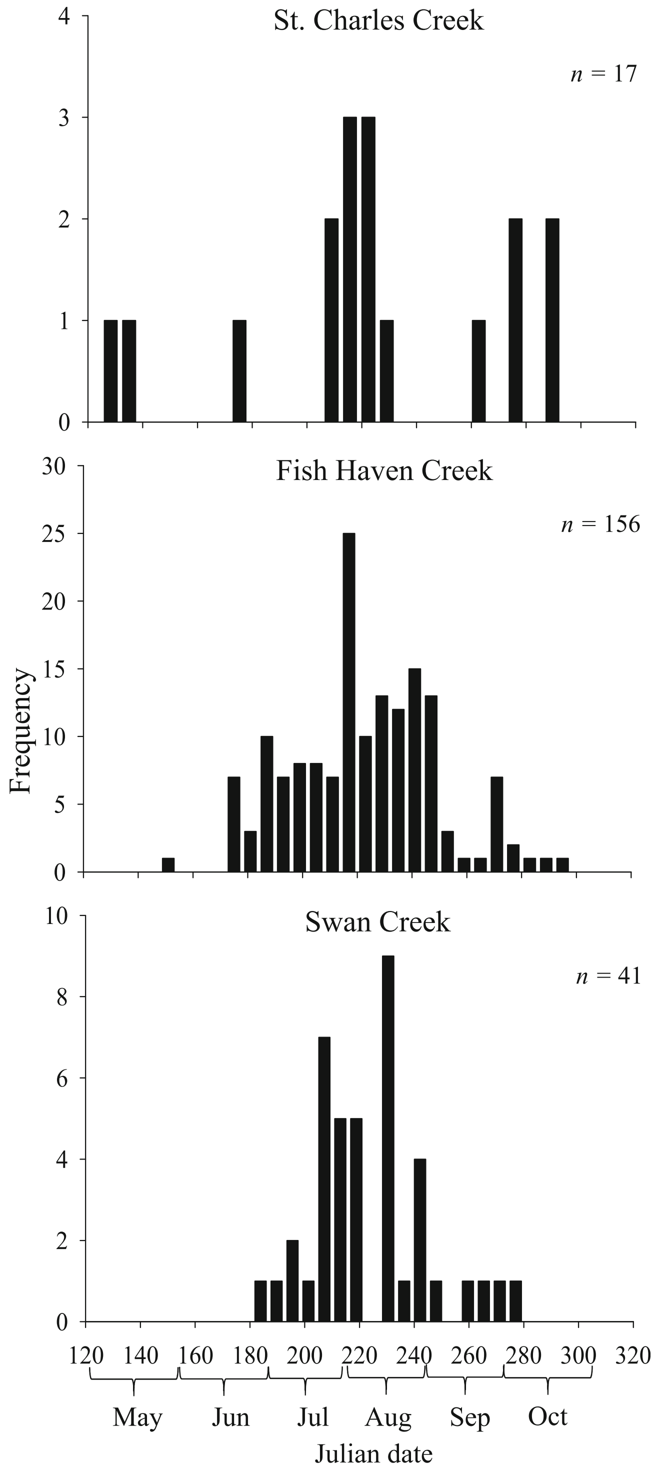

FIGURE 5. Dates on which PIT-tagged Bonneville Cutthroat Trout were detected out-migrating from three tributaries to Bear Lake, Idaho–Utah, during 2019 and 2020.

completely absent from the widest sample sites in British Columbia. Additionally, it is important to recognize that capture efficiency is often highest in stream sections with narrow widths (Rosenberger and Dunham 2005). Although BCT may have escaped capture in wider stream sections, the relationship with stream width is largely a function of the Big Arm of St. Charles Creek. Specifically, average wetted stream width of the Big Arm was approximately three to six times greater than those of the other stream systems. In addition to width, instream habitat in the Big Arm of St. Charles Creek was largely unsuitable for BCT. Reaches in the Big Arm of St. Charles Creek were homogeneous, wide, deep runs with high proportions of fine substrate; these reaches had little canopy cover, low gradient, and warm water temperatures.

Competition between native and nonnative trout is well documented and is a factor in the decline of Cutthroat Trout throughout the western United States (Behnke 1992; Quist and Hubert 2004). The invasion of Brook Trout is considered one of the greatest threats to the persistence of native Cutthroat Trout, particularly in high-elevation streams (Dunham et al. 2002; Hilderbrand and Kershner 2004; Peterson et al. 2008). Brook Trout often compete for resources and frequently displace Cutthroat Trout (Hilderbrand and Kershner 2004; Peterson et al. 2008). Brook Trout were absent in Fish Haven and Swan creeks but common in St. Charles Creek. Total length of Brook Trout in St. Charles Creek varied from 32 to 350 mm, and catch rates varied from 0.00 to 2.62 fish/min. In general, Brook Trout were most abundant in downstream reaches, particularly in the Little Arm of St. Charles Creek. Further evaluations on the potential for negative interactions of Brook Trout with BCT in St. Charles Creek seem warranted.

Out-migration characteristics of BCT in tributaries to Bear Lake have not been previously documented, and little is known about out-migration of other adfluvial populations of trout. Prior research has suggested that adfluvial Cutthroat Trout often out-migrate as age-0 fish in other systems (Raleigh and Chapman 1971; Knight et al. 1999; Campbell et al. 2018), potentially in response to lack of suitable rearing habitat (Chapman 1966). Knight et al. (1999) found that when age-0 BCT did not immediately out-migrate to Strawberry Reservoir, Utah, fish stayed in the tributaries for 1–2 years before out-migration. In a study of Bear Lake, Ruzycki et al. (2001) hypothesized that BCT opted to stay in tributaries for 1–2 years. They argued that Bear Lake is oligotrophic and young out-migrants would likely experience slow growth and prolonged susceptibility to predators. Our results support this contention, as age of BCT was positively associated with out-migration in Swan Creek and length of BCT was positively related to out-migration in St. Charles and Fish Haven creeks. Bonneville Cutthroat Trout may out-migrate during their first year, but we were unable to determine whether BCT were out-migrating immediately after emergence. If BCT out-migrated during their first

TABLE 4. The top logistic regression models investigating the probability of out-migration of PIT-tagged Bonneville Cutthroat Trout among stream reaches ($n = 75$) sampled during 2019 and 2020. Akaike's information criterion adjusted for small sample size (AIC_c) was used to rank the candidate models. Only candidate models within 2.00 AIC_c units of top model were retained. Delta AIC_c (ΔAIC_c), total number of parameters (K), model weight (w_i), and McFadden's pseudo-R^2 are included. Direction of effect for each covariate is indicated (positive [+] or negative [−]).

Stream	Response variable	Model parameters	AIC_c	ΔAIC_c	K	w_i	R^2
St. Charles Creek	Movement	+ Length − Distance to lake	101.3	0.00	3	0.80	0.26
Fish Haven Creek	Movement	+ Length − Diversions	328.2	0.00	3	0.74	0.22
Swan Creek	Movement	+ Age − Distance to lake	177.8	0.00	3	0.62	0.19

year, age-3 and younger BCT would likely be common during surveys in Bear Lake. Results from extensive gill netting in Bear Lake indicate that most BCT in the lake are age 2 and older. We also found that BCT were more likely to out-migrate when tagged in close proximity to Bear Lake. A similar pattern was observed for adfluvial juvenile Lahontan Cutthroat Trout *O. clarkii henshawi* in Summit Lake, Nevada (Campbell et al. 2018). The authors hypothesized that short migration distances for adults were energetically advantageous; thus, adfluvial juveniles were concentrated in downstream reaches (Jonsson et al. 1997; Campbell et al. 2018). Fluctuations in water depth were the most important predictor of Lahontan Cutthroat Trout out-migration, and most fish out-migrated during high streamflows. Similarly, Berger and Gresswell (2009) reported that the majority of Cutthroat Trout in coastal streams in the Umpqua River basin, Oregon, out-migrated between January and May during high stream discharge. In the current study, BCT out-migration occurred most frequently during periods of low flow that overlapped with the irrigation season (i.e., early July to early September). Seven irrigation diversions occur in St. Charles Creek, five diversions are present in Fish Haven Creek, and two diversions occur in Swan Creek. Entrainment in irrigation canals may influence survival and out-migration dynamics of fish (Lindgren and Spencer 1939; Carlson and Rahel 2007) and was considered a major impediment to production of wild BCT in the study tributaries. Given the results of this study, efforts to screen irrigation canals are likely a major factor contributing to the increase of wild BCT in Bear Lake. As previously noted, probability of out-migration of BCT was negatively related to the number of downstream irrigation diversions in Fish Haven Creek. Consequently, additional attention may be needed to prevent entrainment in that system.

The highest proportion of out-migrating BCT occurred in Fish Haven Creek, and the lowest proportion of out-migrating BCT occurred in St. Charles Creek. A variety of factors may explain the low proportion of fish out-migrating from St. Charles Creek. For instance, distance to Bear Lake was negatively associated with BCT out-migration. Kershner (1995) hypothesized that BCT in higher-elevation sites within Bear Lake tributaries are mostly following a resident life history strategy and may not out-migrate. As such, shorter systems (e.g., Swan and Fish Haven creeks) may produce more out-migrants than longer systems. Biotic characteristics may also be responsible for the pattern. High densities of Brook Trout and hybrids in St. Charles Creek may be negatively influencing BCT survival (Hilderbrand and Kershner 2004; Peterson et al. 2008). Additionally, a study conducted on St. Charles Creek in 2007 estimated that 63% of BCT were hybrids (Campbell et al. 2007). The documented ecology of hybrids in Bear Lake does not suggest an adfluvial life history; thus, they may not have genetic cues to out-migrate. Although we avoided tagging obvious phenotypic hybrids, some of the fish in St. Charles Creek may have been hybrids, thereby resulting in low out-migration rates from St. Charles Creek. However, the Big Arm of St. Charles Creek becomes wide and sinuous in its downstream reaches and becomes marsh-like before entering Bear Lake. Avian predators (i.e., American white pelicans *Pelecanus erythrorhynchos*, double-crested cormorants *Phalacrocorax auritus*, and belted kingfishers *Megaceryle alcyon*) were commonly observed near the Big Arm of St. Charles Creek. Avian predators are a widely recognized source of fish mortality (Teuscher et al. 2015), particularly in stream reaches with little instream and canopy cover (Penaluna et al. 2016). Our findings for St. Charles Creek emphasize the value of continued efforts that serve to provide a better understanding of how out-migration changes in response to management actions (i.e., removal of nonnative fishes, habitat alteration, avian predator management).

This study is the first attempt to document the early life history characteristics and out-migration patterns of juvenile adfluvial BCT in the Bear Lake system. Our findings highlight the importance of continued conservation and habitat restoration efforts to ensure the persistence of a species of conservation concern. Additional research and long-term monitoring of BCT in the Bear Lake system would provide a better understanding of out-migration patterns and the role of habitat characteristics over a longer temporal scale. Generally, Fish Haven Creek, Swan Creek, and the main stem of St. Charles Creek contained suitable habitat for BCT. However, low distribution, abundance, and number of out-migrating BCT were evident in lower reaches of St. Charles Creek. Unmitigated threats, such as negative interactions with nonnative species (e.g., competition, hybridization), habitat loss, habitat fragmentation, and agricultural practices (e.g., water diversions, flow reductions), still pose risks to the distribution and abundance of BCT. Despite the ongoing threats, BCT were widely distributed in tributaries. Furthermore, the increased contribution of wild fish to Bear Lake in the past decade is encouraging for the persistence of this important species and can help guide conservation efforts elsewhere.

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