Production of Wild Bonneville Cutthroat Trout in Bear Lake: Evaluation of a Harvest Fishery

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Authorization to Submit Thesis

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Dedication

This work is dedicated to my parents. Their unwavering support throughout my years of pursuing a career in fisheries has been a guiding beacon and has allowed me to follow my dreams. Thank you, a million times over.

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Chapter 1: General Introduction

Bonneville Cutthroat Trout (BCT) *Oncorhynchus clarkii utah* is one of fourteen subspecies of Cutthroat Trout *Oncorhynchus clarkii* and is a species of high ecological and social importance. Bonneville Cutthroat Trout is a species of conservation concern in the states of Idaho and Utah. Bonneville Cutthroat Trout was historically widespread in lentic and lotic systems in the Bonneville basin of Idaho, Nevada, Wyoming, and Utah. During the 1900s, European settlement began in the Bonneville basin and BCT were overexploited in many systems (Behnke and Zarn 1976; Behnke 1992; Lentsch et al. 2000). Additionally, anthropogenic disturbances resulted in an overall loss of suitable habitat for BCT (Lentsch et al. 2000; Teuscher and Capurso 2007; Williams et al. 2009). Overexploitation and loss of habitat for BCT was particularly evident in Bear Lake and its tributaries. Bear Lake is a large, natural, oligotrophic lake located in southeastern Idaho and northern Utah. Four endemic fishes occur in Bear Lake and BCT is the only trout species native to the system. Bonneville Cutthroat Trout in Bear Lake is the only population to follow an adfluvial life history strategy in Idaho (Wurtsbaugh and Hawkins 1990; Behnke 1992; Teuscher and Capurso 2007). Three main spawning tributaries flow into the lake: St. Charles and Fish Haven creeks in Idaho, and Swan Creek in Utah. Nonnative fishes were introduced into the Bear Lake system in the mid 1900s (i.e., Lake Trout *Salvelinus namaycush*, Brook Trout *S. fontinalis*, Rainbow Trout *Oncorhynchus mykiss*) and have likely contributed to the decline in abundance and distribution of BCT. The population of BCT in Bear Lake was considered extirpated by the 1950s (Kershner 1995; Lentsch et al. 2000). In response to the population decline, Utah Division of Wildlife Resources (UDWR) began stocking hatchery BCT in 1973.

Additionally, harvest of wild BCT was closed in 1998 and current regulations allow for the daily harvest of two hatchery fish. In the last decade, efforts to improve the population of wild BCT focused on habitat restoration for adfluvial fish in tributaries to Bear Lake. Habitat restoration projects have been largely successful and the proportion of wild BCT in Bear Lake has increased from 5% in 2002 to 70% in 2017. In recent years, a change in harvest regulations to allow for the harvest of wild BCT has been proposed. However, gaining a more comprehensive understanding of the population dynamics and ecology of BCT in Bear Lake and its tributaries is necessary before changes are made to the management of the fishery. Additionally, this research will provide insight on continued habitat restoration efforts and conservation actions. The objectives of my research were to: (1) evaluate ecology and early life history characteristics of BCT in St. Charles, Fish Haven, and Swan creeks; and (2) describe the population dynamics of wild and hatchery BCT in Bear Lake, and evaluate different management options.

Thesis Organization

This thesis is divided into four chapters. Chapter two describes Bonneville Cutthroat Trout distribution, abundance, and outmigration characteristics in relation to abiotic and biotic factors in three tributaries to Bear Lake. Chapter three describes the population dynamics and harvest management of Bonneville Cutthroat Trout in Bear Lake. Chapter four provides general conclusions and recommendations in relation to the management of Bonneville Cutthroat Trout.

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Chapter 2: Occurrence, Abundance, Movement, and Habitat Associations of Bonneville Cutthroat Trout in Three Tributaries to Bear Lake

Abstract

Bonneville Cutthroat Trout (BCT) *Oncorhynchus clarkii utah* in Bear Lake, Idaho-Utah, is an important recreational species and plays a vital ecological role in systems throughout the basin. Although the distribution and abundance of BCT has declined due to anthropogenic disturbances, production of wild BCT has increased over the last decade as a result of extensive habitat improvement in spawning tributaries. The objective of this study was to assess the occurrence, distribution, and outmigration 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 (TL) of BCT varied from 22 mm to 650 mm and the average TL was 117 mm (SE = 2.2 mm). Regression models were used to identify abiotic and biotic features associated with BCT distribution, abundance, and probability of outmigration. A variety of small- and large-scale habitat characteristics best predicted the occurrence of BCT in St. Charles and Fish Haven creeks. Regardless of the tributary, elevation was negatively related to BCT occurrence or relative abundance. Other habitat characteristics associated with the presence and abundance of BCT were similar to 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 outmigrating 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).

Introduction

Cutthroat Trout *Oncorhynchus clarkii* is an ecologically and socially important species that has a widespread distribution in North America (Behnke 1992, 2002). Bonneville Cutthroat Trout (BCT) *O.c. utah* is one of fourteen subspecies of Cutthroat Trout and is native to the Bonneville Basin of Idaho, Nevada, Utah, and Wyoming. It is a species that warrants protection and conservation due to its importance in many aquatic ecosystems, as well 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 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 (ESA) 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 ESA listing, BCT are considered a sensitive species by the U.S. Forest Service and U.S. Bureau of Land Management, and a species of high conservation priority by the states of Idaho and Utah.

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 early in the 1900s. By the 1950s, the BCT fishery was overexploited in Bear Lake 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 *Oncorhynchus mykiss* and Lake Trout *Salvelinus namaycush* were introduced to 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). 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. 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 (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 last 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 2003; 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 2003). Human land-use practices and anthropogenic disturbances often reduce the quantity and quality of habitat (Horan 2003; Rich et al. 2003). Habitat complexity is vital to a fish's ability to recover from disturbance, escape predation, supply necessary food resources, and provide important rearing habitat (Horan 2003; 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 2003; Heckel et al. 2020). Unfortunately, the ecology and early life history characteristics of BCT in tributaries to Bear Lake is 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 outmigration characteristics is critical to better understanding adfluvial BCT in the Bear Lake system. As such, the specific objectives of this study were to *i)* investigate the distribution and relative abundance of Bonneville Cutthroat Trout in tributaries to Bear Lake, *ii)* assess the relation between habitat characteristics and Bonneville Cutthroat Trout distribution and abundance, and *iii)* evaluate characteristics associated with Bonneville Cutthroat Trout outmigration to Bear Lake. These findings will help 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 Creek, Fish Haven Creek, and Swan Creek (Figure 2.1). Big Spring Creek was excluded from the study due to the presence of an earthen dam ~2 km upstream from Bear Lake that blocks movement of fishes 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 mainstem of St. Charles Creek flows through forested riparian habitat with high gradient and stream velocity near its headwaters. The upper portion of the mainstem is dominated by large substrate types (i.e., boulders and cobble). The lower portion of the mainstem is characterized by moderate gradient and stream velocity, gravel substrate, and riparian habitat composed mostly of Willow *Salix* spp. alongside agricultural fields. The Big Arm of St. Charles Creek carries approximately 75% of the mainstem's discharge (U.S. Forest Service, unpublished data). The Big Arm is relatively wide, 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. The Little Arm is mostly channelized in its lower reaches and is characterized by low gradient and velocity, fine substrate, and abundant aquatic vegetation. Both the Big and Little Arms 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, and 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 Willow 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 global positioning system (GPS) and marked with surveyor's tape. Due to logistical issues (e.g., lack of landowner permission and boat access), several randomly selected sites were omitted from the Big Arm of St. Charles Creek.

Fishes were sampled in each reach using a battery-powered backpack electrofishing unit (model LR 24, Smith-Root Inc; Vancouver, WA). 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 end of each reach; otherwise reaches terminated at a transition between macrohabitats (Meyer and High 2011). Due to depth constraints in five reaches on the Big Arm of St. Charles Creek, a generator-powered electrofishing unit (Infinity model, Midwest

Lake Electrofishing; Polo, MO) 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, RI). Sampling began with 30-Hz pulsed DC, 12% duty cycle, and 100 V. If these settings were ineffective at eliciting a response, 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) was recorded as the time when electricity was applied to the water.

Sampled fishes were identified and total length (TL) was measured to the nearest millimeter. Rainbow Trout × Cutthroat Trout hybrids (hereafter referred to as hybrids) were identified as having similar phenotypic traits to 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 just dorsal to the lateral line. Scales were placed in coin envelopes and transported to the laboratory for processing. To evaluate outmigration, all BCT longer than 70 mm were tagged in the abdominal cavity with 12-mm half duplex (HDX) passive integrated transponder (PIT) tags (Oregon RFID, Portland, OR) following standard methodology (Achord et al. 1993; Bateman et al. 2009). Previous research suggests that juvenile salmonids have PIT tag retention rates over 90% (Meyer et al. 2011; Ostrand et al. 2011; Foldvik and Kvingedal 2018). In addition to stream surveys that included habitat assessments, electrofishing surveys were conducted in an effort to increase sample size for tagged BCT; all fish sampled during these surveys were not included in 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, CA) and Google Earth (Google, Mountain View, CA). 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, CO) 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). Dominate substrate composition was classified using a modified Wentworth scale as: 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 Loggers, Cape Cod, MA) was deployed at each stationary antenna (see antenna description below), as well as in the headwaters, at the midpoint, and 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 they were 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 that 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, the mean coefficient of variation (CV) of velocity, canopy cover, depth, and width was calculated (CV = 100 × [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 area (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 outmigrating to Bear Lake were also created (e.g., age and length of tagged fish, number of downstream diversions).

Scales from sampled BCT were transported to the University of Idaho for processing. Scales 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, MD). 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 in Yellowstone Lake, Wyoming (Laakso 1955). 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 one year when BCT had more than six circuli before the formation of a first annulus (Laakso 1955).

To monitor outmigration of PIT-tagged BCT, stationary half-duplex (HDX) passive integrated transponder (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. I 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 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 outmigrated to Bear Lake. Each HDX antenna consisted of a 142-L cooler (Grizzly, Decorah, IA), two to four 12-V batteries (connected in parallel; Sun Xtender Solar Batteries, West Covina, CA), and a HDX PIT tag data logger (Oregon RFID, Portland, OR). Each antenna station had one or two 140-W solar panels (Solartech Power, Inc., Ontario, CA) 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 mainstem 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 the months of June-October in 2019 and the months of May-October in 2020. Beginning in mid-July to early-August 2020, the antenna on Swan Creek worked intermittently due to technical issues but was resolved 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.

The catch-per-unit-effort ([CPUE]= fish/minute of electrofishing) of BCT was standardized to 100 m of stream length (Meyer et al. 2016). Relative abundance and occurrence of BCT was 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-scale). The probability of outmigration of BCT in the study streams was investigated by using logistic regression.

Models were constructed using the GLM function in program R (R Development 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 one indicated 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 one minus the difference in the log likelihood of a model with parameters and the intercept-only model (McFadden 1974). McFaddens 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 three large-scale variables and eighteen small-scale variables (Table 2.1). Models predicting the probability of outmigration of BCT included twenty-two abiotic and biotic variables and 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 to 35 candidate models for each submodel.

All models for occurrence, relative abundance, and probability of outmigration 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 *K*. All models within two AIC_c or $QAIC_c$ 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 et al. 2005; Meyer and High 2011).

Results

In St. Charles Creek, 1,833 individual fish representing 11 different species were sampled, including 404 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 (68.7%) 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 (mainstem, Big Arm, Little Arm). Bonneville Cutthroat Trout occurred at 86% of the reaches on the mainstem, 13% of reaches on the Big Arm, and 80% of reaches on the Little Arm (Figure 2.1). 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 relatively similar across the three study streams. The average length of BCT in St. Charles Creek was slightly smaller (mean ± SE; 109 ± 3.0 mm) than in Fish Haven (130 ± 3.9 mm) and Swan creeks (131 ± 4.2 mm; Figure 2.1). Catch rates were highest in Swan Creek (0.67 ± 0.11 fish/min) followed by St. Charles (0.19 ± 0.03 fish/min) and Fish Haven creeks (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 2.2). Mean lengths at age at time of capture of BCT were relatively similar between the three tributaries, particularly at age 1 (Figure 2.3).

Abiotic and biotic characteristics were highly variable among the three tributaries (Table 2.1). Regression models suggested that habitat characteristics related to BCT occurrence differed from those associated to relative abundance (Table 2.2). 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 since 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 (Table 2.2). 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). Three hundred and eleven 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 outmigration from the three tributaries (Figure 2.4). The proportion of BCT that outmigrated from St. Charles Creek (5.5%) was lower than for Fish Haven (50.2%) and Swan (16.3%) creeks. In general, the mean length of outmigrating BCT was 25% greater than the mean length of fish that were PIT tagged (Figure 2.5). Average length of BCT outmigrating in Swan Creek was the largest of the three tributaries (184 ± 4.1 mm) followed by St. Charles (170 ± 2.4 mm) and Fish Haven creeks (148 ± 3.7 mm). Of the BCT that were tagged in St. Charles Creek, ages varied from 1 to 6 years. Ages of tagged BCT varied from 1 to 7 years in Fish Haven Creek and from 1 to 5 years in Swan Creek. All ages of BCT that were tagged were detected outmigrating in both St. Charles and Fish Haven creeks, but I did not detect any age-5 fish outmigrating in Swan Creek. Age-1 BCT were the most frequently tagged in all three tributaries and the most common to outmigrate in Fish Haven Creek. Interestingly, age-2 BCT were the most common to outmigrate in St. Charles and Swan creeks (Figure 2.5). The dates of outmigration for BCT in St. Charles Creek were the most widely distributed with detections beginning in early May and ending in early October. The range of outmigration dates in Fish Haven and Swan creeks was narrower. Bonneville Cutthroat Trout began outmigrating in June and low numbers of BCT continued outmigrating into the fall. The peak of BCT outmigration occurred in August in all three study streams (Figure 2.6).

Abiotic and biotic factors related to the probability of BCT outmigration varied between the three tributaries. The probability that a fish outmigrated was positively associated with fish length for St. Charles and Fish Haven creeks (Table 2.3). The probability that fish outmigrated 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 outmigration of BCT was positively associated with fish age and negatively associated with distance to Bear Lake (Table 3).

Discussion

Persistence of fishes is largely influenced by the availability 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. 2011; Ertel et al. 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 research indicated that large-scale abiotic factors such as gradient, elevation, and stream size were associated with the occurrence of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in northwestern Wyoming (Kruse et al. 1997) and Westslope Cutthroat Trout *O.c. 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 homogenous 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. Previous studies suggest that habitat complexity and heterogeneity positively influence Cutthroat Trout occurrence and abundance (Harvey et al. 1999; Rosenfold 2000; Berger and Gresswell 2009; Smith et al. 2015). 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 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 (Rosenfold 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. Stream width was an important factor in models assessing the occurrence and abundance of BCT. Rosenfold (2000) found that stream width had a negative relationship with presence of juvenile Cutthroat Trout and fish were often completely absent from the widest sample sites in British Columbia. Additionally, capture efficiency was likely higher in narrow stream sections (Heckel et al. 2020) and fish may have escaped capture in wider sections where BCT were not detected. Canopy cover was an important variable for BCT occurrence in tributaries to Bear Lake. Canopy cover is critical for providing refuge from overhead predators and for regulating stream temperature (Penaluna et al. 2015; 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 (Harvey et al. 1999; Gowan 1996; Berger and Gresswell 2009; Young 2011). In my 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 nonwoody cover in sites where BCT were present. This suggests that all instream cover is important, but woody cover may be most important to BCT. A variety of abiotic and biotic characteristics were important in predicting the distribution and abundance of BCT in the tributaries to Bear Lake. In general, I found similarities across the three tributaries, but it is worth highlighting differences associated with the Big Arm of St. Charles Creek. Habitat in the Big Arm of St. Charles Creek was largely unsuitable for BCT. Reaches in the Big Arm of St. Charles Creek were homogenous, wide, deep runs with high proportions of fine substrate. 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 BKT in St. Charles Creek varied from 32 to 350 mm and catch rates varied from 0.00 to 2.62 fish per minute. In general, BKT were most abundant in downstream reaches, particularly in the Little Arm of St. Charles Creek. Further evaluations on the potential for negative interactions of BKT with BCT in St. Charles Creek seem warranted.

Outmigration characteristics of BCT in tributaries to Bear Lake have not been previously documented and little is known about outmigration of other adfluvial populations of trout. Prior research has suggested that adfluvial Cutthroat Trout often outmigrate 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 outmigrate to Strawberry Reservoir, Utah, fish stayed in the tributaries for 1–2 years before outmigration. In Bear Lake, Ruzycki and Wurtsbaugh (2001) hypothesized that BCT opted to stay in tributaries for 1–2 years. They argued that Bear Lake is oligotrophic and young outmigrants would likely experience slow growth and prolonged susceptibility to predators. My results support the contention Ruzycki and Wurtsbaugh (2002) where age was positively associated with outmigration in Swan Creek, and length of BCT was positively related to outmigration in St. Charles and Fish Haven creeks. Bonneville Cutthroat Trout may outmigrate during their first year, but I was unable to determine whether BCT were outmigrating immediately after emergence. If BCT outmigrated during their first year, age-3 and younger BCT would likely be common during surveys in Bear Lake. Results from extensive gill netting in Bear Lake (see Chapter 3) indicate that most BCT in the lake are age 2 and older. I also found that BCT were more likely to outmigrate when tagged in close proximity to Bear Lake. A similar pattern was observed for adfluvial juvenile Lahontan Cutthroat Trout (LCT) *O. C. henshawi* in Summit Lake, Nevada (Campbell et al 2018). The authors hypothesized that short migration distances for adults was energetically advantageous; thus, adfluvial juveniles were concentrated in downstream reaches (Jonsson et al. 1997; Campbell et al. 2018). Fluctuations in water depth was the most important predictor of LCT outmigration and most fish outmigrated during high stream flows. Similarly, Berger and Gresswell (2009) reported that the majority of Cutthroat Trout in coastal streams in the Umpqua River basin, Oregon, outmigrated between January and May during high stream discharge. In the current study, BCT outmigration 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 in Fish Haven Creek, and two in Swan Creek. Entrainment in irrigation canals may influence survival and outmigration 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 outmigration 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 outmigrating BCT occurred in Fish Haven Creek and the lowest proportion of outmigrating BCT occurred in St. Charles Creek. A variety of factors may explain the low proportion of fish outmigrating from St. Charles Creek. For example, biotic characteristics may be responsible for the pattern. High densities of BKT and hybrids in St. Charles Creek may be negatively influencing BCT survival. 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 outmigrate. Although I avoided tagging obvious phenotypic hybrids, some of the fish in St. Charles Creek may have been hybrids. Additionally, distance to Bear Lake was negatively associated with BCT outmigration. Kershner (1995) hypothesized that BCT in higher elevation sites in Bear Lake tributaries are mostly following a resident life history strategy and may not outmigrate. The Big Arm of St. Charles becomes wide and sinuous in its downstream reaches and becomes “marsh-like” before entering Bear Lake. Avian predators (i.e., American Pelicans *Pelecanus erythrorhynchos*, Double-crested Cormorants *Phalacrocorax auritus*, Belted Kingfishers *Megaceryle alcyon*) were commonly observed near the Big Arm of St. Charles Creek. Avian predators are a widely recognized source of mortality of fishes (Teuscher et al. 2015), particularly in stream reaches with little instream and canopy cover (Penaluna et al. 2015).

This study is the first attempt to document the early life history characteristics and outmigration patterns of juvenile adfluvial BCT in the Bear Lake system. My 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 outmigration patterns and the role of habitat characteristics over a longer temporal scale. Generally, Fish Haven, Swan, and the mainstem of St. Charles creeks contained suitable habitat for BCT. However, low distribution, abundance, and number of outmigrating 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 last decade is encouraging to the persistence of this important species.

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Table 2.1. Mean and standard error (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 occurrence, relative abundance, and probability of outmigration of Bonneville Cutthroat Trout (BCT) candidate models. Outmigration variables were used in probability of BCT outmigration candidate models only.

		Stream				
Variable	**Description**	**St. Charles Creek**			**Fish Haven Creek**	**Swan Creek**
		Mainstem	**Little Arm**	**Big Arm**		
	Large-scale variables					
Elevation	Elevation (m) of the upstream end of the stream reach	1883.09 (17.3)	1813.40 (0.87)	1810.5 (1.10)	2012.35 (23.11)	1825.00 (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	8255.55 (695.99)	2016.00 (188.48)	3950.13 (1113.72)	4522.70 (441.36)	647.00 (92.60)
	Small-scale variables					
Reach area	Total area of stream reach (m^2)	1148.33 (114.00)	1079.98 (228.52)	6271.19 (1395.04)	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	Catch-per-unit-effort for BKT in reaches	0.23 (0.05)	1.22 (0.48)	0.11 (0.11)	-	-
Length	Total length (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 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)

0

Table 2.2. 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-Akaike's information criterion ($QAIC_c$) was used to rank the candidate models. Only candidate models within 2.00 AIC_c or $QAIC_c$ 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, [-] negative).

Response variable	Model parameters	AIC_c or $QAIC_c$	ΔAIC_c or $\Delta QAIC_c$	K	w_i	R^2
St. Charles Creek						
	Large-scale models					
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
	Large-scale models					
Relative abundance	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						
	Large-scale models					
Presence-absence	− 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
	Large-scale models					
Relative abundance	− 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						
	Large-scale models					
Relative abundance	− 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

Table 2.3. The top logistic regression models investigating the probability of outmigration of Bonneville Cutthroat Trout tagged with passive integrated transponder tags 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 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, [−] negative).

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

Table 2.4. Sum of Akaike weights (*w*) and direction of relationship (positive or negative) for each independent variable in top logistic regression models investigating presence-absence and relative abundance of Bonneville Cutthroat Trout among stream reaches (n = 75) sampled during 2019 and 2020.

Stream	**Independent variable**	***w***
	Presence-absence	
St. Charles Creek		
	Depth_{CV}	(+) 0.93
	Distance to lake	(+) 0.51
	Canopy cover	(+) 0.50
	Cover area	(+) 0.48
	Elevation	(−) 0.42
	Width	(−) 0.31
	Gradient	(+) 0.29
Fish Haven Creek		
	Fine substrate	(−) 0.75
	Cover area	(+) 0.51
	Elevation	(−) 0.42
	Temperature	(+) 0.41
	Distance to lake	(−) 0.26
	Velocity_{CV}	(+) 0.24
	Relative abundance	
St. Charles Creek		
	Width	(−) 0.75
	Canopy cover_{CV}	(+) 0.22
	Canopy cover	(−) 0.22
Fish Haven Creek		
	Distance to lake	(−) 0.57
	Elevation	(−) 0.43
	Gradient	(−) 0.33
Swan Creek		
	Elevation	(−) 0.65
	Velocity	(−) 0.64
	Gradient	(−) 0.19
	Distance to lake	(−) 0.17

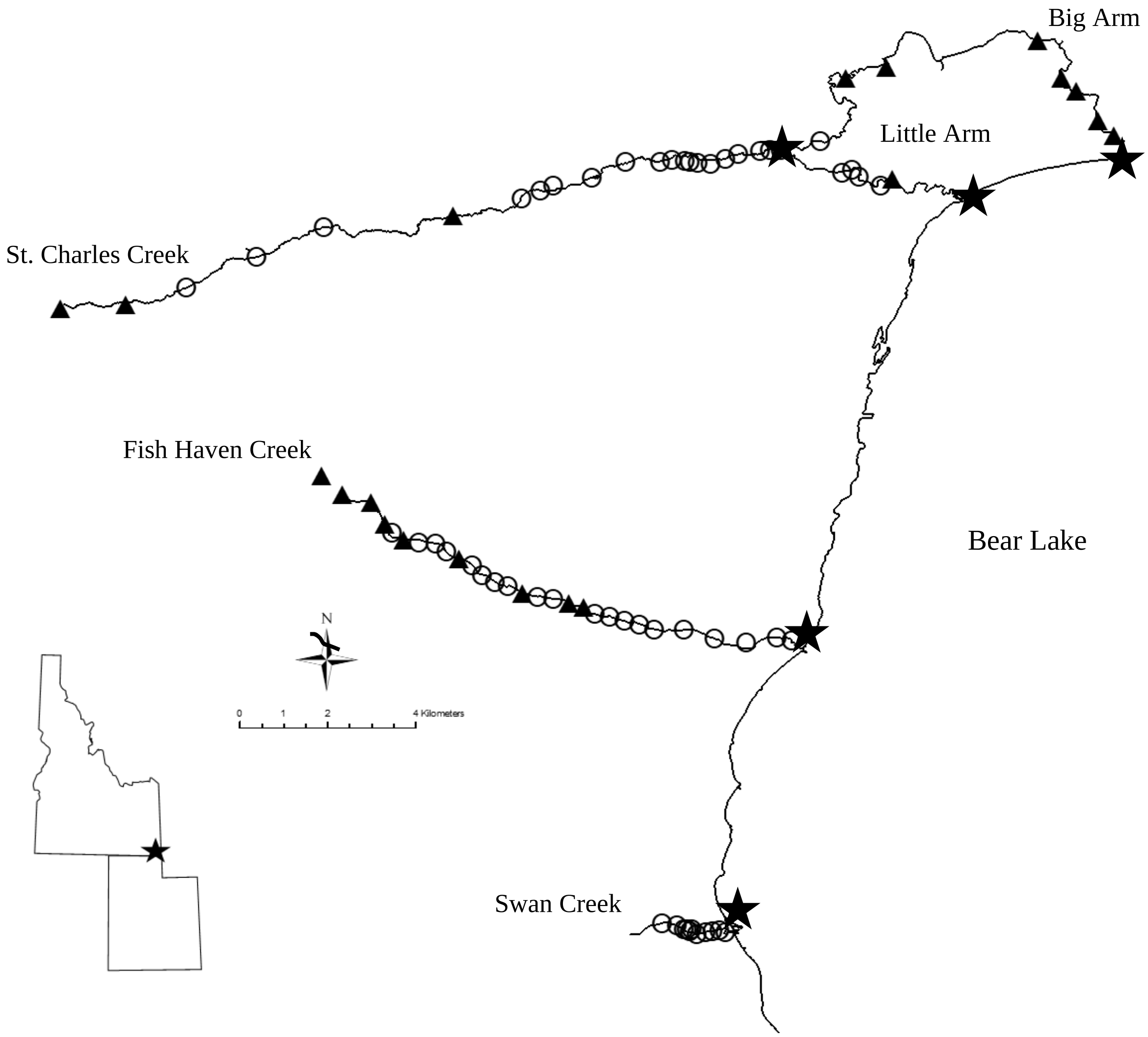

Figure 2.1. Tributary sites where habitat assessments and electrofishing surveys conducted during 2019 and 2020 in three tributaries to Bear Lake, Idaho-Utah. Stream sites where BCT were present are symbolized by hollow circles and sites where BCT were absent are symbolized by black triangles. Passive integrated transponder tag antennas are symbolized by black stars.

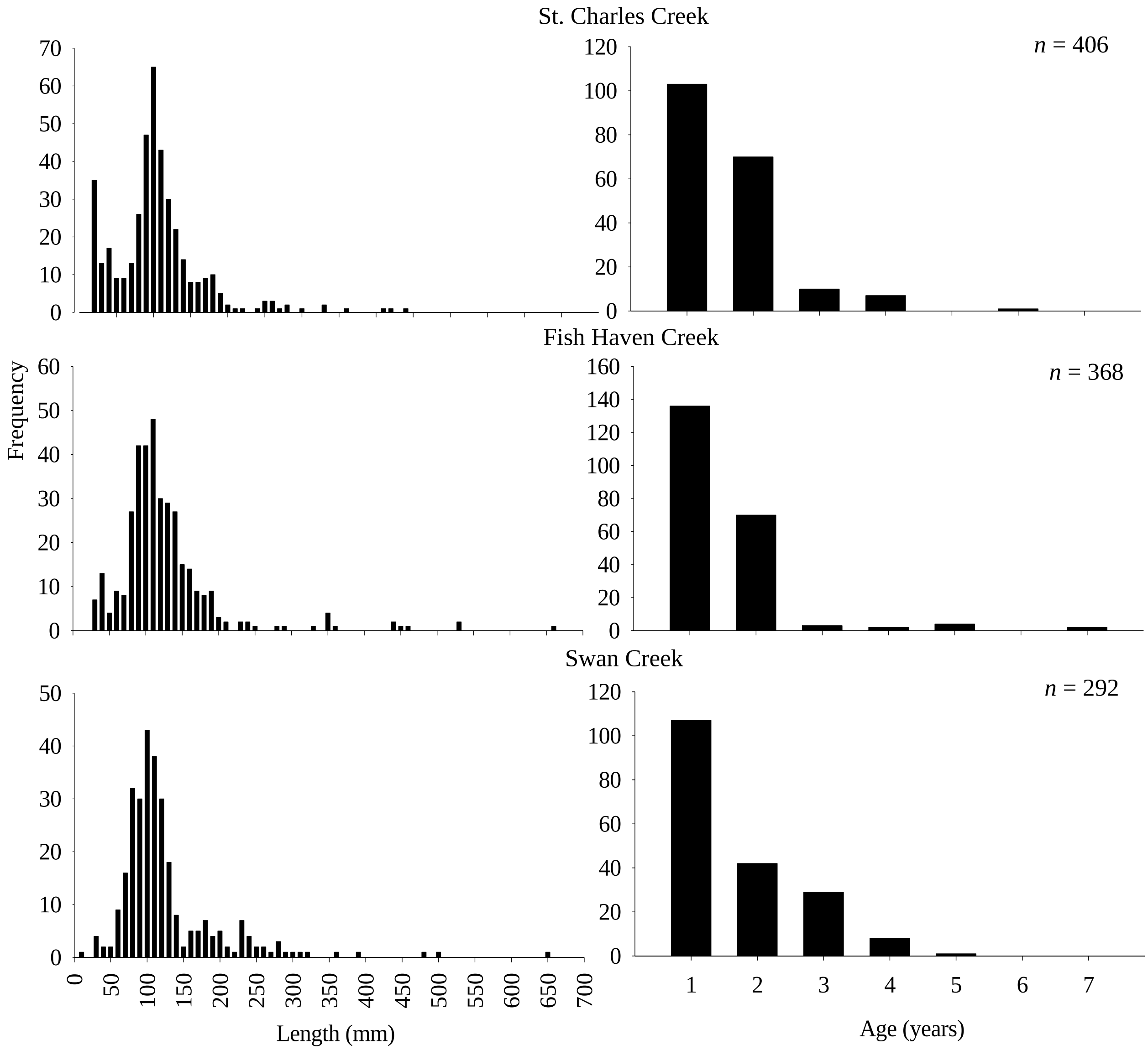

Figure 2.2. Age- and length-frequency distributions of Bonneville Cutthroat Trout sampled in tributaries to Bear Lake, Idaho-Utah, during 2019-2020.

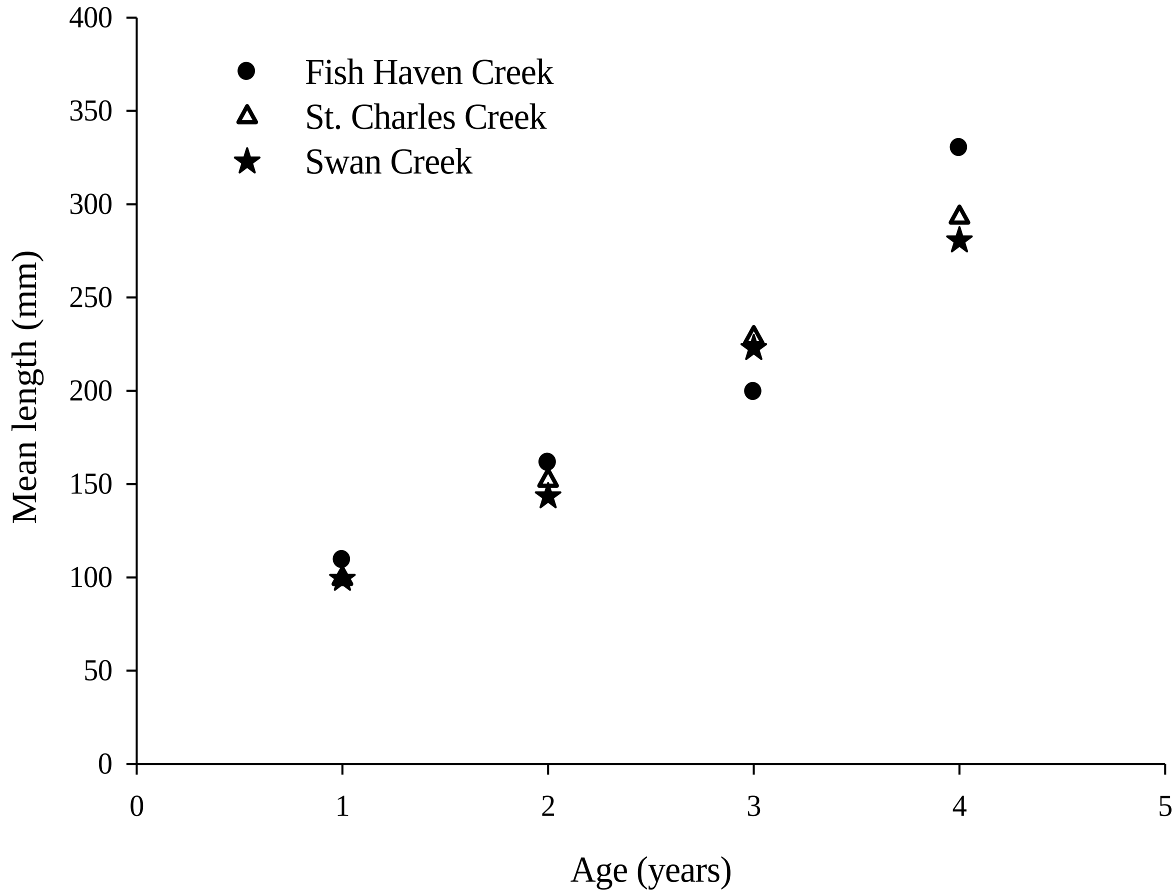

Figure 2.3. Mean length at age at time of capture for Bonneville Cutthroat Trout sampled in tributaries to Bear Lake, Idaho-Utah, during 2019 and 2020.

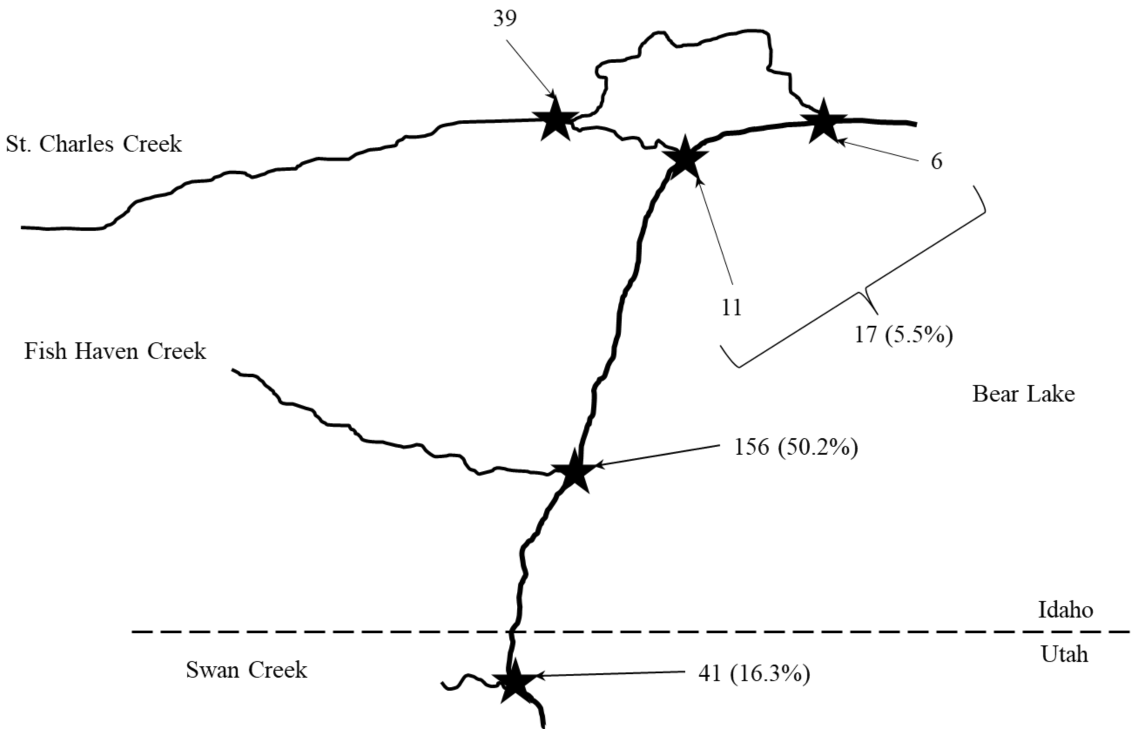

Figure 2.4. Number and proportion (in parentheses) of BCT detected at stationary passive integrated transponder antennas during downstream outmigration on three tributaries to Bear Lake, Idaho-Utah during 2019 and 2020.

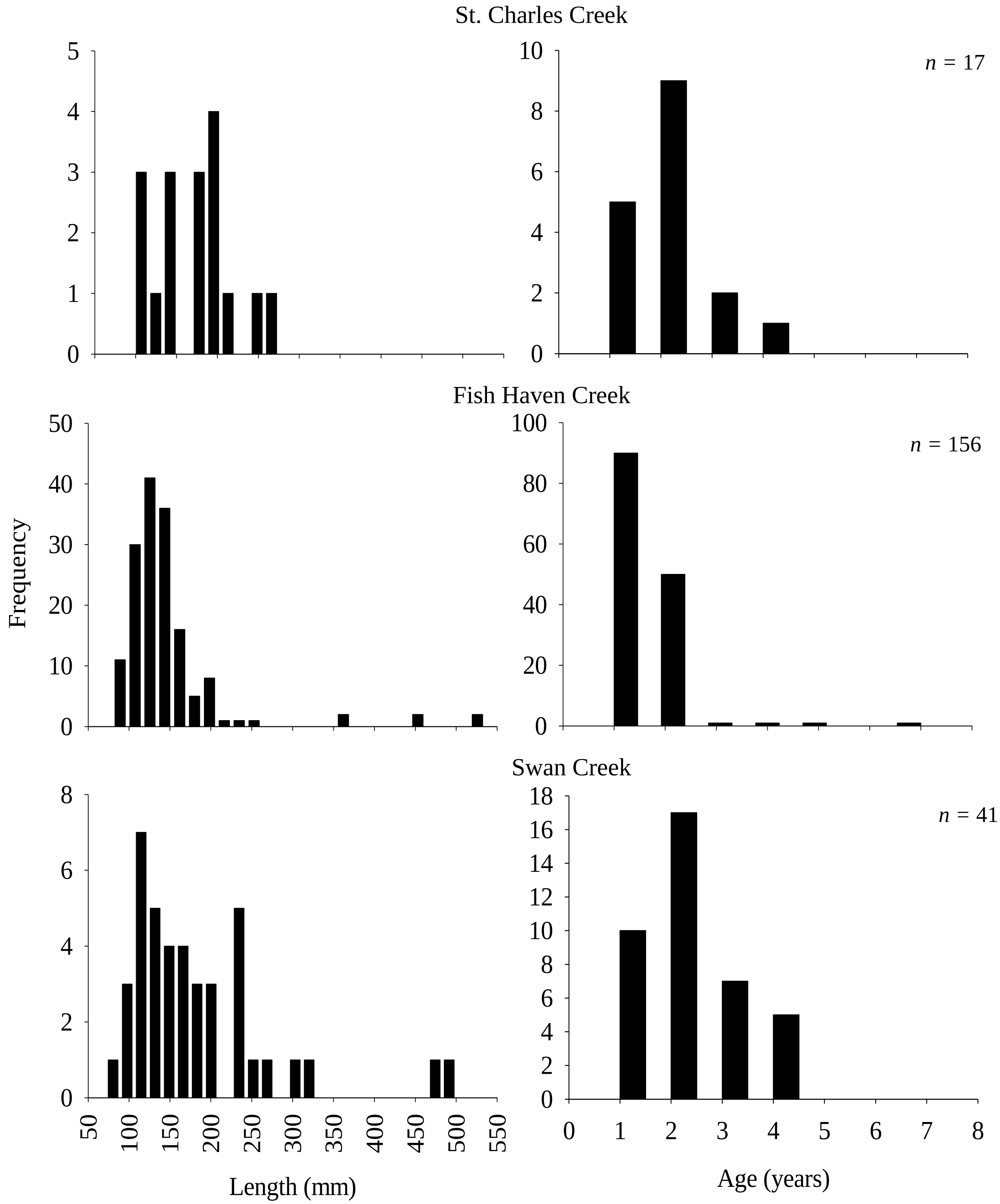

Figure 2.5. Age-and length-frequency distributions of passive integrated transponder-tagged Bonneville Cutthroat Trout detected outmigrating at stationary antennas located at the mouth of three tributaries to Bear Lake, Idaho-Utah, during 2019 and 2020.

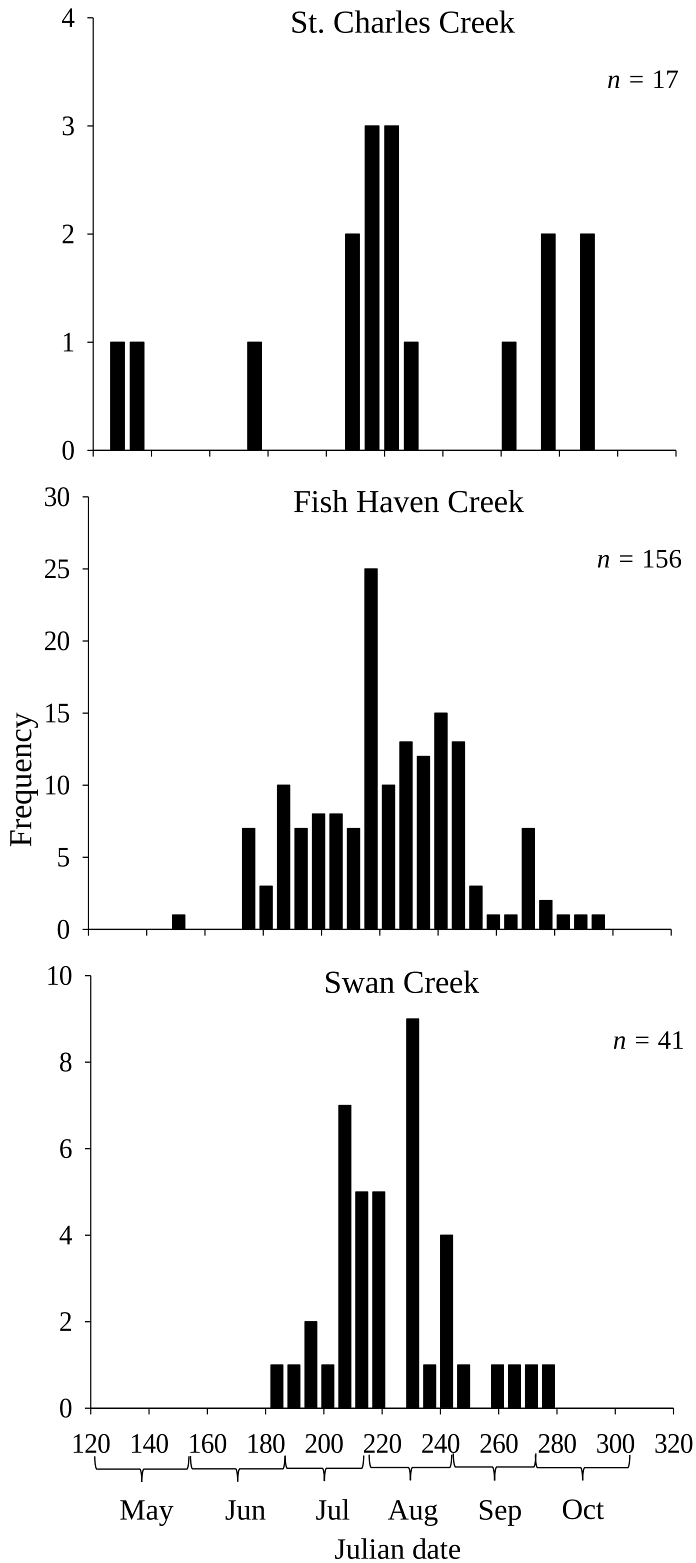

Figure 2.6. Date passive integrated transponder-tagged Bonneville Cutthroat Trout were detected outmigrating from three tributaries to Bear Lake, Idaho-Utah, during 2019 and 2020.

Chapter 3: Population Dynamics and Harvest Management of the Bonneville Cutthroat Trout Fishery in Bear Lake

Abstract

Land-use disturbances and associated losses in habitat quantity and quality negatively affected the Bonneville Cutthroat Trout (BCT) *Oncorhynchus clarkii utah* population in Bear Lake in the early 1900s. Bear Lake BCT follow an adfluvial life history strategy and without access to suitable spawning habitat, the population of wild BCT was nearly extirpated by the early 1950s. In response to this decline, supplementation of the population with hatchery BCT began in 1973. Production of wild BCT was minimal until conservation efforts shifted towards improving fish habitat and access to spawning tributaries. In 2002, only 5% of the population was wild fish and by 2017 nearly 70% of BCT in annual population surveys were wild. As a result, rule changes have been proposed to allow for regulated harvest of wild BCT. However, gaining a comprehensive understanding of the population dynamics of BCT in Bear Lake is critical before changes are made to management of the fishery. The objectives of this study were to describe the population dynamics of wild and hatchery BCT in Bear Lake and evaluate different management options. We evaluated population demographics of hatchery and wild BCT in Bear Lake and used age-structured population models to assess a variety of management scenarios associated with wild fish harvest regulations (e.g., bag limits). Bonneville Cutthroat Trout grew at relatively fast rates and females began to mature at age 5. I observed considerable differences in the length and age structure of the hatchery population (i.e., exploited) versus the wild population (i.e., unexploited) of BCT. In general, BCT in Bear Lake were larger and older than Cutthroat

Trout in other systems. The current rate of exploitation for hatchery BCT was estimated as 0.27 (i.e., two daily fish limit). If the limit were changed to a six-daily fish limit, the rate of exploitation would be approximately 0.47. A yield-per-recruit model evaluating spawning potential ratio indicated that a two wild fish limit would be a sustainable level of exploitation, whereas a six wild fish limit would result in recruitment overfishing. This research has provided baseline population dynamics of BCT in Bear Lake that will provide insight for future monitoring efforts. Under current conditions, allowing harvest of either origin BCT in Bear Lake would satisfy angler values while ensuring the persistence of an important population.

Introduction

Rehabilitation of wild Bonneville Cutthroat Trout (BCT) *Oncorhynchus clarkii utah* has been a focus of fishery management in the last decade (Hilderbrand and Kershner 2000; Teuscher and Capurso 2007; Budy et al. 2020). Bonneville Cutthroat Trout were historically abundant and widespread in the Bonneville basin in Idaho, Nevada, Wyoming, and Utah. Over the last century, the distribution and abundance of BCT has declined due to overharvest, negative interactions with nonnative fishes, and anthropogenic disturbances that altered habitat. Due to the decline in distribution and abundance, BCT is of conservation concern in the states of Idaho and Utah. The importance of managing BCT for ecological and recreational benefits is typified at Bear Lake, Idaho-Utah.

Bear Lake is a large, natural, oligotrophic lake spanning the Idaho-Utah border and is generally dimictic (Ruzycki et al. 2001). A pumping facility on the north shore of Bear Lake connects the lake to its outlet while generating hydropower and manipulating water levels for irrigation purposes. The population of BCT in Bear Lake was thought to be nearly extirpated by the early 1950s due to loss of habitat and overexploitation (Kershner 1995). A variety of characteristics of BCT in Bear Lake make the population unique. For example, BCT in Bear Lake are predominantly piscivorous and grow to large sizes (Kershner 1995). Additionally, it is the only population of BCT in Idaho to follow an adfluvial life history strategy (Wurtsbaugh and Hawkins 1990; Behnke 1992; Teuscher and Capurso 2007). Bear Lake is also unique and contains a variety of native and nonnative fishes. Four endemic fishes occur in Bear Lake: Bear Lake Whitefish *Prosopium abyssicola*, Bonneville Whitefish *P. spilotnotus*, Bonneville Cisco *P. gemmifer*, and Bear Lake Sculpin *Cottus extensus*. The four endemic species are an important prey resource for BCT (Ruzycki et al. 2001). Nonnative species include Lake Trout *Salvelinus namaycush*, Brook Trout *S. fontinalis*, and Rainbow Trout *Oncorhynchus mykiss.* Lake Trout were first stocked in Bear Lake in 1911, but the origin of Brook Trout and Rainbow Trout in the system is unknown. Bonneville Cutthroat Trout in Bear Lake are adfluvial, access to suitable spawning and rearing habitat in tributaries is critical to their life history. St. Charles, Fish Haven, and Swan creeks are considered the main spawning tributaries for BCT in Bear Lake (see Chapter 2). Habitat degradation and lack of access in these tributaries due to anthropogenic disturbances (i.e., irrigation practices, road construction) and potential negative interactions with nonnative fishes resulted in low production of wild BCT in the 1900s and early 2000s. In response to a declining population, a spawning weir was constructed by Utah Division of Wildlife Resources (UDWR) on Swan Creek in 1973 and is the source for 150,000-300,000 juvenile BCT that are stocked into Bear Lake annually (Teuscher and Capurso 2007). An agreement between the Idaho Department of Fish and Game (IDFG) and UDWR states that most progeny taken from wild fish at the weir must be reared and then stocked into Bear Lake. Harvest of wild BCT was closed in 1998 in Bear Lake and angling is prohibited in tributaries and fish staging locations (i.e., 274 m surrounding tributaries entering the lake) during winter and spring (December – June). Current fishing regulations allow for the daily harvest of two hatchery BCT (identifiable by a clipped adipose fin) in Bear Lake and two BCT of either origin in tributaries. In recent years, conservation efforts have focused on restoring habitat (i.e., improving fish passage, reducing entrainment) in tributaries for adfluvial BCT.

Habitat restoration efforts in tributaries were largely successful and a marked increase in the contribution of wild BCT to the Bear Lake fishery has been observed in recent years.

For example, the proportion of wild fish in 2002 gill netting surveys was 5% and increased to 70% by 2017. Additionally, the catch-per-unit effort (CPUE = number of BCT/gill-net hour) increased during the same period (Scott Tolentino, UDWR, unpublished data). The shift in the proportion of wild and hatchery fish has been noticed by the angling community and anglers have shown interest in the opportunity to harvest wild fish. As a result of the change in the population, IDFG and UDWR have considered changing regulations to allow for the harvest of wild fish in Bear Lake. However, lack of information regarding population dynamics of BCT in Bear Lake prompted this investigation.

Understanding fish population dynamics is critical for making informed and effective management decisions (Ricker 1975; Allen and Hightower 2010). Growth, recruitment, and mortality are the three rate functions governing fish populations (Ricker 1975). Fish growth is one of the most important factors that can provide insight on individuals and populations. For instance, growth analyses provide insight on reproductive ecology (e.g., age at maturity, fecundity), vulnerability to predation, and time to achieve important sizes (e.g., “trophy” lengths; Allen and Hightower 2010). Recruitment is also a critical component of fish population dynamics. Recruitment is often a main governing function of a population and quantifying recruitment is vital to the evaluation of fish populations (Ricker 1975; Quist 2007). Mortality is another vital component of fish population dynamics. Total mortality in exploited populations is comprised of natural mortality (e.g., disease, predation) and fishing mortality (Ricker 1975; Allen and Hightower 2010; Pope et al. 2010). Natural mortality is difficult to manage, whereas fishing mortality can be influenced with harvest regulations (Allen and Hightower 2010; Isermann and Paukert 2010). Collectively, population dynamics influence changes in abundance and structure of a population over time (Pope et al. 2010).

The study of exploited populations often involves developing models that combine data from rate functions (i.e., growth, recruitment, mortality) with other factors that influence fish populations (i.e., sex ratio, fecundity) to provide insight on the potential outcomes of various management decisions (Ricker 1975; Pope et al. 2010; Ng et al. 2016; McCormick and High 2020). In particular, age-structured models are useful for evaluating how a population responds to different harvest scenarios. Although population trends have been monitored with standardized annual netting in Bear Lake, information on population rate functions is unavailable. Additionally, very little is known about the life history of this unique population of BCT. The objectives of my research are to describe the life history and population dynamics of wild and hatchery BCT in Bear Lake, and to evaluate different management options associated with establishing a harvest fishery for wild BCT.

Methods

Sampling for BCT was conducted in partnership with UDWR following their annual survey design. Fish were sampled using gill nets at fixed sites to provide estimates of relative abundance and composition (i.e., hatchery or wild) during 2017-2020 (Figure 3.1). Each site was sampled three times per year: pre-stratification (spring), stratification (summer), and post-stratification (fall). Monofilament experimental gill nets were 48.7 m long, 1.8 m deep, and had ten panels with 12.7-, 19.1-, 25.4-, 38.1- and 50.8-mm bar-measure mesh. Seven sinking nets were set at varying depths (i.e., 5, 10, 15, 20, 25, 35, and 50 m deep) at each site. Nets were set perpendicular to shore. After fishing for 24 hours, all fishes were removed from nets. Each net was reset for an additional 24 hours, resulting in a total set time of 48 hours per location. I conducted a supplemental sampling event in September of 2019 and July of 2020 to provide additional BCT population data and evaluate the efficiency of a different gill net design (i.e., suspended gill net). Seven experimental gill nets were constructed to replicate gill nets used by UDWR to sample Bonneville Cutthroat Trout in Strawberry Reservoir, Utah. The monofilament gill nets were 53.3 m long, 6.1 m deep, and had seven panels with 12.7-, 19.1-, 25.4-, 38.1-, 50.8-, 63.5-, and 76.2-mm bar-measure mesh. Nets were initially set at randomly selected sites, but catch rates were very low. As such, subsequent samples was focused in areas with a history of catching BCT. Respective mesh size and method of capture (i.e., entangled, wedged, gilled) were recorded for BCT in gill net surveys to evaluate selectivity (Millar and Fryer 1999; Klein et al. 2019). Catch rates of BCT during these surveys were too low to effectively model selectivity, but they did provide additional BCT for the study.

All BCT captured in gill nets were measured for total length (nearest 1.0 mm) and weight (nearest 0.1 g). Fish origin was identified (i.e., hatchery or wild) based on the presence or absence of an adipose fin. Sex and maturity were evaluated based on size, shape, and appearance of gonads (Downs et al. 1997). Sagittal otoliths were removed from all BCT, cleared of excess tissue, and stored in coin envelopes (Quist et al. 2012; Long and Grabowski 2017).

Once in the laboratory, otoliths were mounted in epoxy (Koch and Quist 2007) and sectioned with an IsoMet Low Speed Saw (Buehler, Lake Bluff, IL) along the dorsoventral plane following methods in Long and Grabowski (2017). Thinly sliced sections were further polished if necessary to improve overall clarity. Sections were aged under a dissecting scope using transmitted light and the distance between observed annuli was measured with Image-

Pro Plus software using standard methodologies for annulus identification (Media Cybernetics, Rockville, MD; Quist et al. 2012; Long and Grabowski 2017).

All analyses were conducted separately for hatchery and wild BCT to evaluate differences between exploited and unexploited populations. Sampling years and netting surveys were combined since notable differences were not observed across years or gear types. An age-length key was used to estimate the age distribution for all BCT sampled by UDWR from 2017-2020 (Isermann and Knight 2005; Quist et al. 2012). Length structure was summarized using length-frequency histograms and further evaluated using proportional size distribution (PSD; Gabelhouse 1984; Neumann et al. 2012). I estimated PSD values as the number of fish in a specified length category divided by the number of fish greater than or equal to stock (S) length (≤ 200 mm), multiplied by 100. Length categories for BCT included quality (Q; 350 mm), preferred (P; 450 mm), memorable (M; 600 mm), and trophy (T; 750 mm). Based on age-specific catch, age-4 and older fish were considered fully recruited to the gear. A weighted catch curve was used to evaluate total annual mortality (*A*) for age-4 to age-12 fish (Smith et al. 2012).

Mean back-calculated length at age for individual fish was estimated using the Dahl-Lea method:

$$L_i = R_i\left(\frac{L_c}{R_c}\right)$$

where L_i is the length at annulus i, L_c is the length at capture, R_c is the otolith radius at capture, and R_i is the otolith radius at annulus i (Quist et al. 2012; Shoup and Michaletz 2017). Using back-calculated lengths at age, growth rates of BCT were also described using von Bertalanffy growth models:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0}\right]$$

where L_t (mm) is the length at time t (years), L_∞ is the mean asymptotic length, k is the growth coefficient, and t_0 is the theoretical age when length is zero (von Bertalanffy 1938; Ogle 2016; Ogle et al. 2017).

The spawning potential ratio (SPR) of wild BCT under varying exploitation levels was evaluated using a Beverton-Holt yield-per-recruit model (Beverton and Holt 1957; Ricker 1975; Goodyear 1993). The SPR is used to evaluate the effect of varying levels of exploitation on the productivity of females in a population. The SPR is simply the ratio of mature eggs produced at a given level of exploitation divided by the number of eggs that would be produced with no exploitation. A critical SPR level of 0.20 – 0.30 has been shown to protect fish populations from recruitment overfishing (Goodyear 1993; Slipke et al. 2002; Koch et al. 2009). If the SPR was less than 0.20 (i.e., 80% reduction in egg production), then recruitment overfishing may occur and result in a population decline. I constructed models using the Fishery Analysis and Modeling Simulator (FAMS; Slipke and Maceina 2014). All parameters used in the model were derived from the wild population of BCT except for age-0 survival and fecundity estimates (Table 3.1). Because no age-0 BCT were sampled, an estimate of survival of age-0 to age-1 BCT was obtained from the literature (Stapp and Hayward 2002; Janowicz et al. 2018; McCormick and High 2020). I was unable to directly estimate fecundity of BCT in Bear Lake due to low sample size for suitable fish. Therefore, I used the equation (fecundity = $0.0026 \times TL^{2.2255}$) for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Idaho from Meyer et al. (2003). The sex ratio of the wild population was specified as 0.5 since the observed sex ratio did not differ significantly (0.53

female; 95% CI: 0.48-0.58). Using creel data collected by UDWR from Bear Lake, I estimated that 95% of harvested BCT were ≥ 400 mm; therefore, I used 400 mm as the minimum length harvested by anglers. Parameter estimates from the von Bertalanffy growth model, the length-weight relationship (i.e., $\log_{10}$ [weight] - 4.793 + 2.888 × $\log_{10}$ [length]), and estimates from maturity and longevity were also used as inputs to the model.

The wild population of BCT in Bear Lake does not currently experience harvest mortality; therefore, I was able to estimate fishing mortality (*F*) and exploitation (μ) using the difference in *A* for both wild and hatchery fish (Ricker 1975). Using the characterization of a type II fishery, exploitation rate under current harvest regulations (i.e., two daily bag limit) was calculated. I assumed that μ of wild fish would be equal to hatchery fish. Using creel data from 2010 and 2015 in Bear Lake, I estimated the exploitation rate of a six fish daily bag limit by dividing the number of BCT caught, released, and harvested (up to six fish per angler) by the estimated total number of BCT caught, released, and harvested. This value was then multiplied by a correction factor that corrected μ to 0.27 (i.e., a two fish bag limit) using the same creel data. Conditional natural mortality (*cm*) was input to the yield-per-recruit as 0.24 (i.e., *A* for the fish that do not experience harvest). Conditional fishing mortality (*cf*) was varied in the model from 0.00-0.90 in increments of 0.05. For each model iteration, I used 1,000 individuals as the number of recruits. I modeled a "worst-case" scenario that 100% of fish harvested would be of wild origin. Two different harvest scenarios were evaluated using the yield-per-recruit model. More specifically, I evaluated SPR under two- and six-fish daily bag limits for wild BCT. A two-fish BCT limit was evaluated because it would maintain the current bag limit but allow inclusion of wild BCT in the harvest. I also evaluated a six-fish limit as this is consistent with IDFG's general Cutthroat Trout bag limit in southeast Idaho.

Results

During the spring, summer, and fall months of 2017-2020, 807 individual BCT were captured in gill nets in Bear Lake. Average BCT catch rate in gill nets was 0.11 (SE = 0.01) fish/hr and the proportion of hatchery fish sampled (0.47) was less than wild fish (0.53). In general, sampled wild BCT were larger than hatchery fish and varied in length from 190-702 mm (Figure 3.2; mean ± SE; 463 ± 5 mm). Hatchery BCT varied in length from 169 – 640 mm (400 ± 4 mm). The majority of hatchery BCT were between 300 and 475 mm, and most wild BCT were between 350 and 625 mm. Of the stock-length hatchery BCT, most fish were quality length (Figure 3.2). Similarly, most of the stock-length wild BCT were also quality length; wild preferred and memorable-length BCT were more common than for hatchery fish. No trophy-length BCT were sampled.

Age of wild BCT varied from 2-12 years and wild fish were generally older (6.5 ± 0.1 years) than hatchery fish (5.0 ± 0.1 years) whose ages varied from 2-11 years (Figure 3.3). Proportionately, more age-5 and younger hatchery BCT were sampled than wild BCT. In contrast, age-6 and older BCT were more common for wild than hatchery fish. Growth was similar between hatchery and wild fish except that L_∞ was lower for hatchery fish (Figure 3.4). Total annual mortality of age-4 to age-11 hatchery BCT was higher (0.47) than for wild fish (0.24; Figure 3.3). Exploitation of hatchery BCT under current regulations was estimated as 0.27. If the daily bag limit allowed harvest of six wild fish, μ would be approximately 0.47. Females began to mature at age 5 and 100% were mature by age 8. Fecundity of female BCT increased with length and age. Mean fecundity was 2,988.6 (SE = 76.3) eggs and varied from 1,633 to 5,617 eggs per female. Spawning potential ratio of BCT declined as rates of exploitation increased (Figure 3.5). At current levels of exploitation and conditional natural mortality, SPR was above the 0.20-0.30 threshold. If a more conservative SPR of 0.30 is considered, exploitation would likely have to exceed 0.35 to result in recruitment overfishing and a population decline. If a less conservative SPR of 0.20 is adopted, μ could increase to about 0.45 before there are concerns of overfishing.

Discussion

The wild population of BCT in Bear Lake has increased in the last decade, but population demographics and the potential effects of angler exploitation have not been evaluated. This study is the first of its kind to evaluate population dynamics of BCT in general, and adfluvial BCT in particular. Unfortunately, research on population dynamics of adfluvial trout is quite limited, despite the fact such populations are often highly susceptible to environmental perturbations and are of conservation concern (Tennant et al. 2015; Simmons et al. 2020). For example, many migratory populations of Yellowstone Cutthroat Trout have declined while resident populations have generally persisted (Gresswell 2011; Kaeding and Koel 2011). In the current study, I evaluated the population dynamics separately for wild and hatchery BCT in Bear Lake. Marked differences were observed in the age and length structure of hatchery and wild fish, many of which are likely explained by the harvest of hatchery fish. I further assessed the population-level response of exploitation on wild BCT using an age-structured yield-per-recruit model. The model assumed a "worst-case" scenario that 100% of fish harvested would be of wild origin. Results indicated that at current exploitation rates, harvest of wild fish would be sustainable.

Age and length structure of BCT in Bear Lake differed from other populations of Cutthroat Trout. Bear Lake BCT are relatively long lived and attain large sizes. In Bear

Lake, wild and hatchery BCT grew fast during the first few years and then growth declined slightly with age. Similar patterns have been observed in other Cutthroat Trout populations (Gresswell 2011; Janowicz et al. 2018). In the current study, BCT were detected as old as age 12 and attained sizes over 700 mm. Gresswell (2011) reported that Yellowstone Cutthroat Trout in Idaho generally live 8 to 9 years and achieve a maximum length of ~600 mm. However, adfluvial Yellowstone Cutthroat Trout in Henrys Lake, Idaho, had a maximum length of 650 mm and maximum age of 11 (Darcy McCarrick, University of Idaho, unpublished data). Yellowstone Cutthroat Trout in Henrys Lake grew about 16 mm more per year than BCT in Bear Lake during their first two years, but BCT grew an average of 12 mm more per year after their third year. Adfluvial Yellowstone Cutthroat Trout in Yellowstone Lake, Wyoming, had a maximum length of 565 mm and age of 10 years (Kaeding and Koel 2011). In streams and rivers, BCT tend to grow slower and attain smaller sizes than lacustrine fish (Kershner 1995). For example, Janowicz et al. (2018) found Westslope Cutthroat Trout *Oncorhynchys clarkii lewisi* rarely exceeded 260 mm in small Rocky Mountain streams in Canada. Downs et al. (1997) reported Westslope Cutthroat Trout up to age 8 in Montana streams with lengths rarely exceeding 324 mm.

Vital rates are critical to evaluating population models and risk assessment for management practices (Meyer et al. 2003; Pope et al. 2010). Unfortunately, a paucity of information exists regarding the mortality, longevity, and fecundity of BCT. Size at maturity of female BCT in Bear Lake was similar to Yellowstone Cutthroat Trout in Yellowstone Lake (Syslo 2015). All fish were mature at ~500 mm (i.e., age 8 in Bear Lake) in both systems. Meyer et al. (2003) found that 100% of Yellowstone Cutthroat Trout larger than 400 mm and older than age 8 in the South Fork Snake River, Idaho, were mature. Conversely, in stream systems, Westslope Cutthroat Trout reached maturity at age 3 to 5 (Downs et al. 1997). I was unable to directly estimate fecundity of BCT in Bear Lake and used an equation for fecundity of Yellowstone Cutthroat Trout in the South Fork Snake River, Idaho to estimate fecundity. Using the equation, we estimated mean fecundity of Bear Lake BCT at 2,989 eggs per female. Additionally, I approximated fecundity of BCT using an equation for Yellowstone Cutthroat Trout in Yellowstone Lake (Kaeding and Koel 2011). Fecundity estimates using this equation resulted in more eggs per female for wild BCT. Therefore, I opted to use the Meyer et al. (2003) equation due to its more conservative estimate for wild BCT in Bear Lake. Although this approach is likely reasonable for this study, additional work focused on estimating fecundity of BCT in Bear Lake would be useful.

The differences in vital rates observed between hatchery and wild BCT in Bear Lake is likely a function of the fishery on hatchery fish. Although exploitation rates vary, my estimate of exploitation is within the distribution of values reported for western trout fisheries. Schill et al. (2007) reported exploitation rates < 1% for Redband Trout *Oncorhynchus mykiss gairdneri* in eight Idaho desert streams. However, exploitation rates in more accessible and popular Rainbow Trout fisheries in Idaho varied from 2% to 40% (Meyer and Schill 2014). Cox and Walters (2002) reported exploitation rates from 21% to 60% for lacustrine Rainbow Trout fisheries in British Columbia. With regards to total annual mortality, estimates for BCT in Bear Lake (i.e., ~24-47%) were similar to other Cutthroat Trout populations. Simmons et al. (2020) reported that total annual mortality of Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* in Summit Lake, Nevada, was 49%. Janowicz et al. (2018) found similar results for Westslope Cutthroat Trout (A = 43%).

Despite notable differences in the two groups of BCT in Bear Lake, the Beverton-Holt-yield-per-recruit model indicated that the current level of exploitation for hatchery BCT would not likely result in recruitment overfishing of wild BCT. Recruitment overfishing has occured often in freshwater fisheries and management would have been aided by SPR analysis (Slipke et al. 2002). The SPR is a relatively simple index that was first developed for marine fisheries to protect populations from recruitment overfishing (Goodyear 1993). In recent years, SPR has been applied to assess recruitment overfishing in many freshwater systems (Quist et al. 2002; Slipke 2002; Colombo et al. 2007). Goodyear (1993) suggested a critical level of 20-30% SPR in exploited marine populations to avoid recruitment overfishing, but various SPR levels have been considered in other systems. For example, an SPR of 10-20% was found to be adequate for Channel Catfish *Ictalurus punctatus* in the upper Mississippi River (Slipke 2002). A critical SPR level of 20% was used for Silver Carp *Hypophthalmichthys molitrix* to cause recruitment overfishing in the midwestern U.S. (Siebert et al. 2015). Furthermore, an SPR of 40% was suggested for protecting vulnerable Shovelnose Sturgeon *Scaphirhynchus platorynchus* populations in the Missouri River (Quist et al. 2002) and upper Mississippi River (Koch et al. 2002). It is worth noting that yield-per-recruit models do not incorporate the effects of density dependence (Goodyear 1993). Density-dependent processes can influence growth, survival, and other vital rates of fish (Jenkins et al. 1999). Therefore, I also developed a deterministic female-based Leslie matrix that incorporated a density-dependent function on survival (Caswell 2001; McCormick et al. 2021). The Leslie matrix model showed similar results as the Beverton-Holt yield-per-recruit model, but I opted to use the Beverton-Holt model for its simplicity and clarity.

This study provided important insights into the population dynamics of BCT in Bear Lake. Fish grew relatively fast, attained large sizes, and were long-lived in comparison to other populations of Cutthroat Trout. Results from population models indicate that wild BCT in Bear Lake can sustain the current level of exploitation observed for hatchery fish. However, the future of any fish population depends on a variety of abiotic and biotic factors that may not be easily predicted (Ng et al. 2016). Additionally, the critical SPR value associated with the BCT fishery in Bear Lake is unknown and long-term population monitoring will be required to ensure that recruitment overfishing does not occur. Such assessment would not only allow managers to refine population information associated with BCT, but will also provide information to evaluate how population dynamics change in response to harvest. The potential changes in population dynamics of wild fish will likely be noticed in several years after harvest regulations allow for harvest of wild BCT. It is possible that a truncation in the length distribution of wild fish will be noticed within a few years of any regulation changes. Additionally, because wild BCT did not recruit to the gear in annual gillnetting surveys until fish are age 4 and older, effects of harvest on recruitment of BCT might not be detected for four years or more. This study serves as a baseline of BCT population dynamics for future monitoring and can be used to help guide management actions. This research also contributes to a greater understanding of population dynamics regarding adfluvial populations of Cutthroat Trout and the importance of evaluating vital rates to inform harvest management strategies.

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Table 3.1. Parameters used in a spawning potential ratio yield-per-recruit model for the wild Bonneville Cutthroat Trout population sampled from Bear Lake, Idaho-Utah in 2017-2020 via gill nets. Abbreviations used: L_∞ is the mean maximum length, k is the growth coefficient, and t_0 is the theoretical age when length is zero.

Parameter	Value
Von Bertalanffy growth coefficients	L_∞ = 721 mm; K = 0.142; t_0 = 0.688
Maximum age	12 years
Conditional natural mortality	0.24
Conditional fishing mortality	0.0 to 0.90
Log_{10} (weight) : log_{10} (length) coefficients	a = -4.793; b = 2.888
Age at sexual maturation	5 years
Fecundity-to-length relation	-3583.90 + 12.54 (length)
Percent of fish that are females	50% for all age classes
Percent of females spawning annually	15% for age 5; 70% for age 6; 94% at age 7; 100% for age 8 to age 12
Minimum length limit	400 mm total length
Number of recruits	1,000 fish

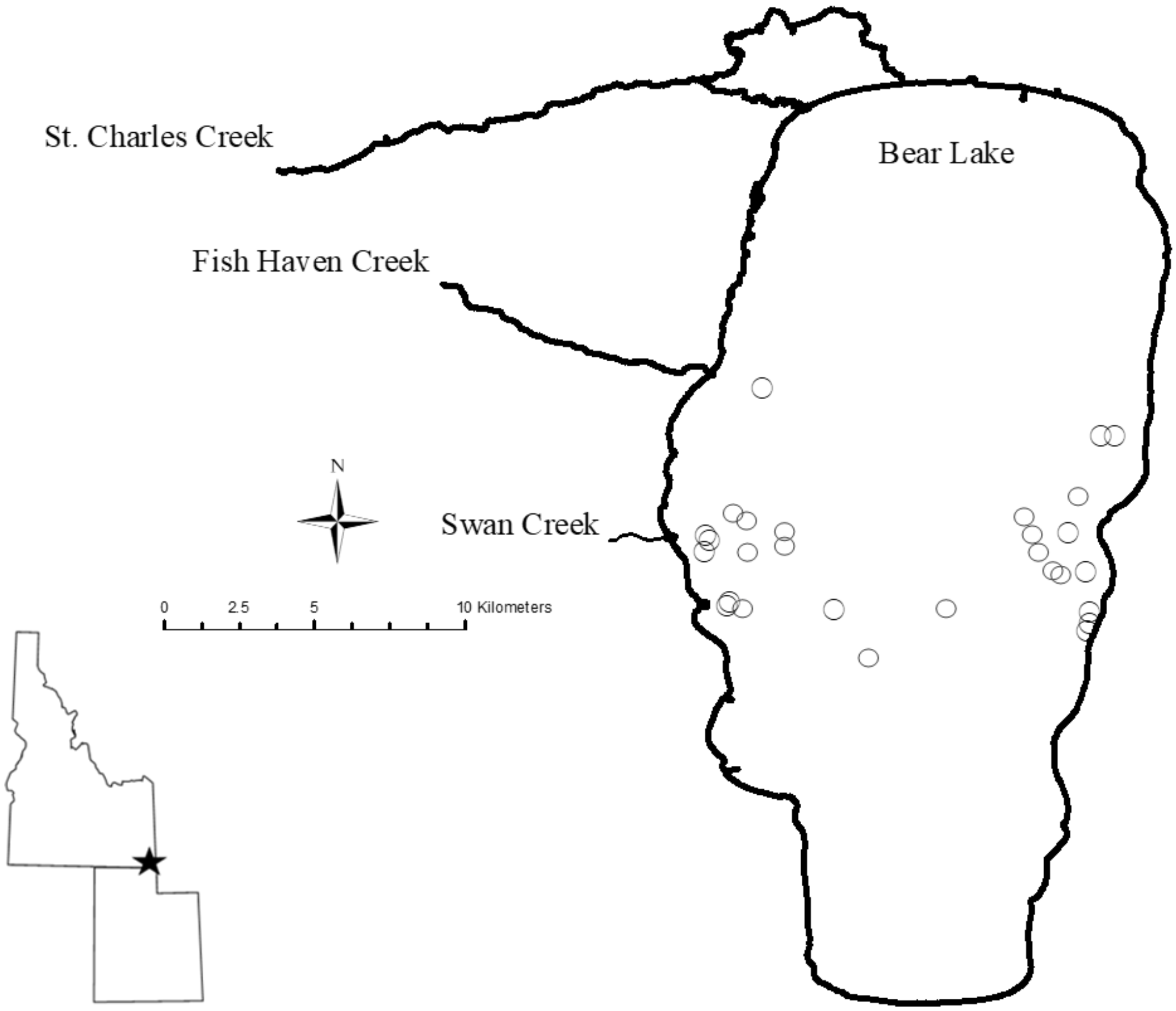

Figure 3.1. Map of Bear Lake, Idaho-Utah, including the three main tributaries. The hollow circles represent gillnetting locations in 2017-2020.

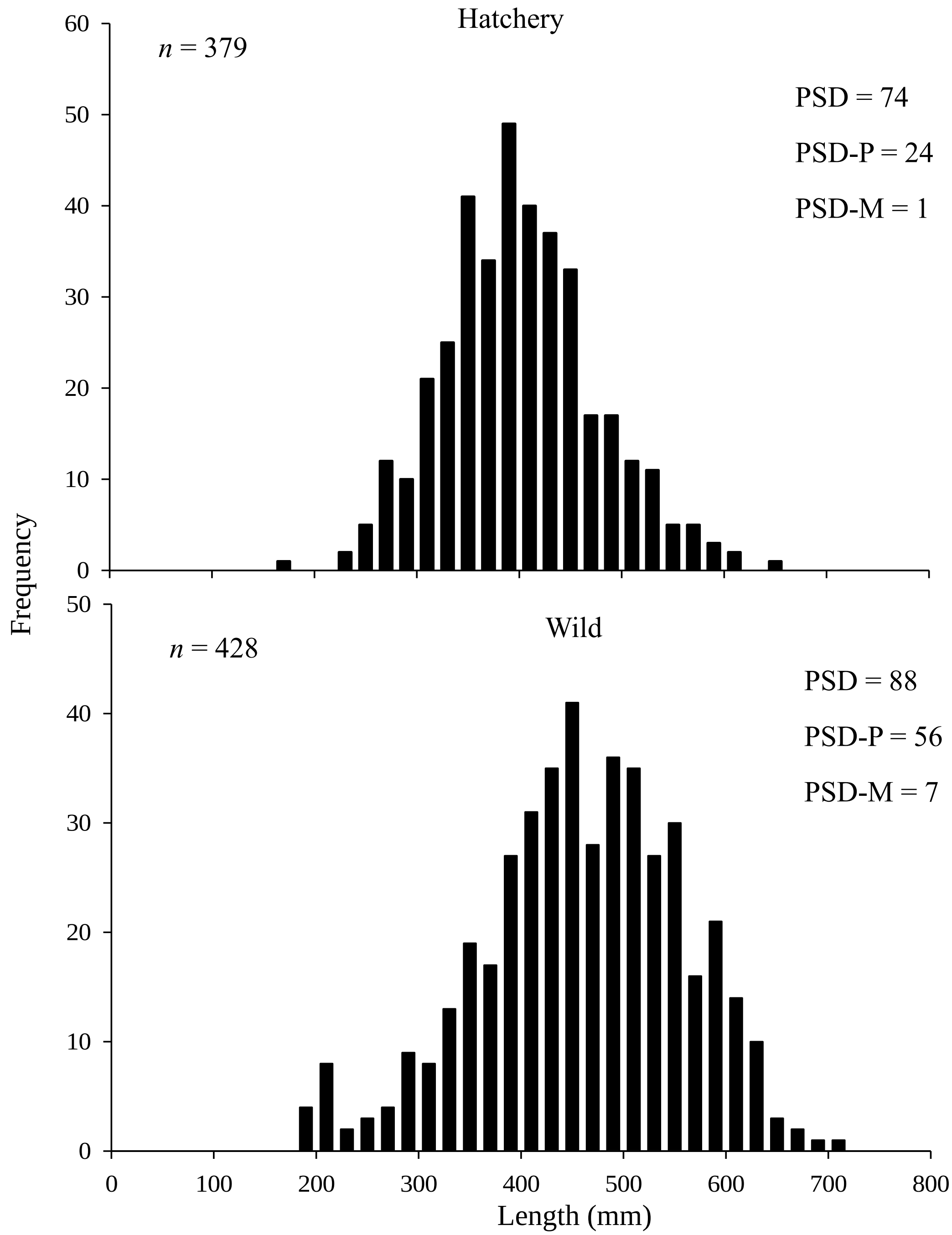

Figure 3.2. Length-frequency distribution of Bonneville Cutthroat Trout sampled from Bear Lake, Idaho-Utah in 2017-2020 via gill nets. Size structure indices include the overall proportional size distribution (PSD) and those of preferred- (PSD-P), memorable- (PSD-M), and trophy-length (PSD-T) fish.

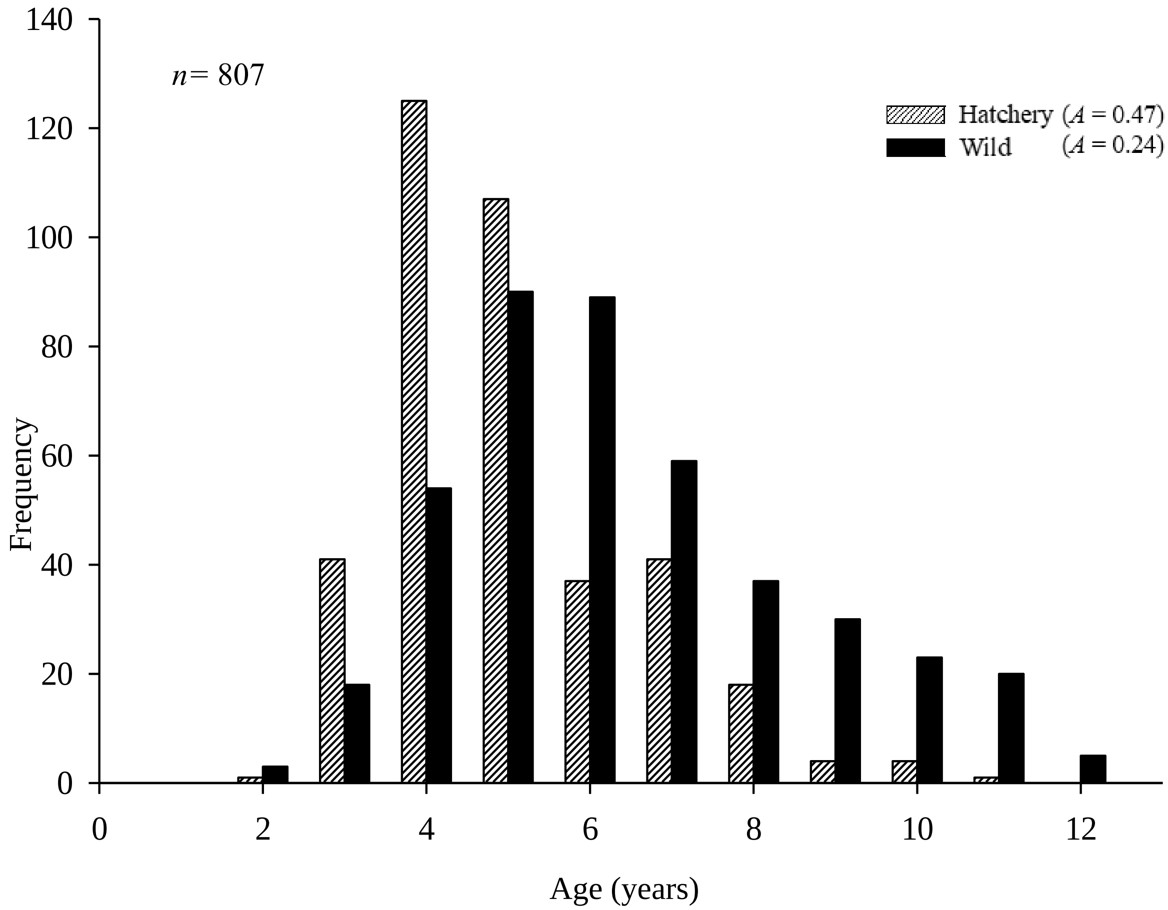

Figure 3.3. Age structure of Bonneville Cutthroat Trout sampled from Bear Lake, Idaho-Utah, in 2017-2020.

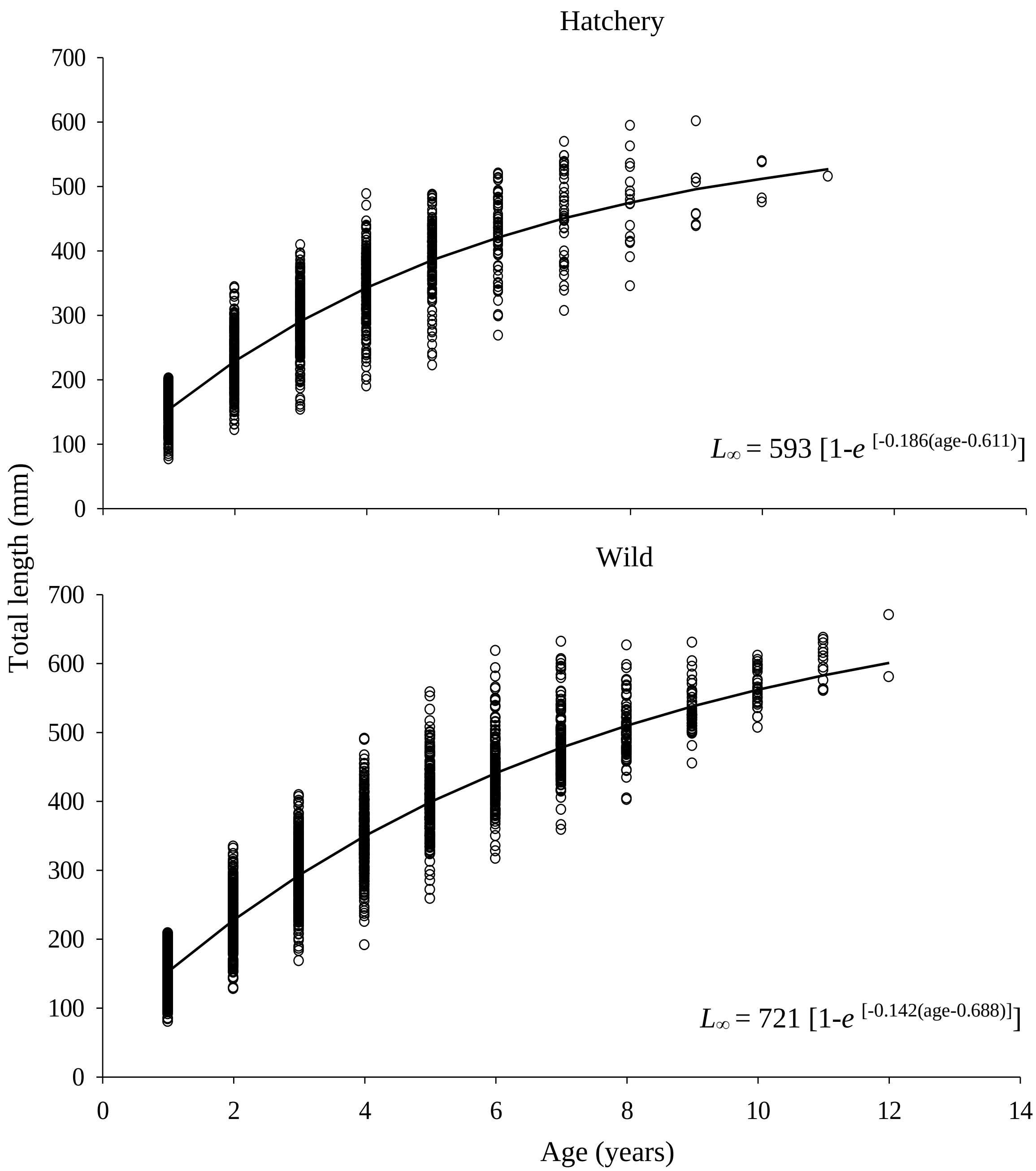

Figure 3.4. Von Bertalanffy growth model fit to length-at-age data for Bonneville Cutthroat Trout sampled from Bear Lake, Idaho-Utah in 2017-2020.

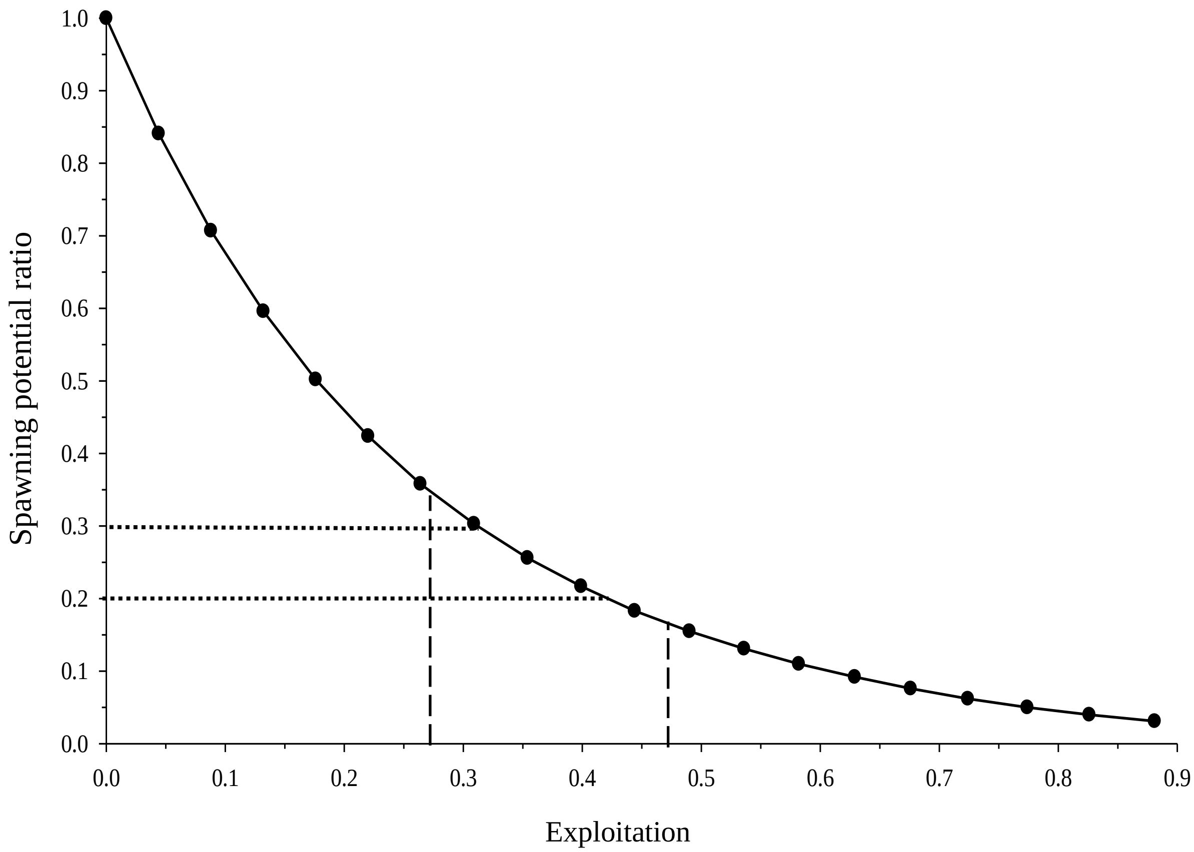

Figure 3.5. Spawning potential ratio of Bonneville Cutthroat Trout in Bear Lake, Idaho-Utah. The dashed lines represent exploitation rates of proposed daily bag limits (i.e., two or six fish limit). The dotted lines represent the range of critical SPR values. Parameter estimates were obtained from Bonneville Cutthroat Trout sampled in 2017-2020.

Chapter 4: General Conclusions

My research contributes to our knowledge on the fundamental ecology and population dynamics of adfluvial Bonneville Cutthroat Trout (BCT) *Oncorhynchus clarkii utah*. More specifically, my work provides insight on the distribution, abundance, habitat relationships, and outmigration characteristics of BCT in tributaries to Bear Lake, Idaho-Utah. Additionally, this study assessed population demographics of BCT in Bear Lake. The overarching goal of this thesis was to highlight the importance of additional habitat restoration efforts to increase production of wild fish in tributaries and inform management decisions related to a wild BCT fishery in Bear Lake. The demographic study paired with population modeling evaluated two different management strategies for a wild BCT fishery in Bear Lake.

The impetus for Chapter 2 was to describe the ecology and characteristics of a unique population of adfluvial BCT in tributaries to Bear Lake. As a result of this research, I learned that BCT are widely distributed in Fish Haven and Swan creeks, and were found in relatively high abundance, particularly in downstream reaches near the lake. High proportions of BCT were detected outmigrating from Fish Haven and Swan creeks, but relatively low proportions were detected moving from St. Charles Creek. In addition to few outmigrants, BCT outmigrating in St. Charles Creek, I found poor habitat and low abundance of BCT in the "Big Arm" and "Little Arm" of St. Charles Creek. Unsuitable habitat (i.e., no canopy cover, wide reaches, fine sediment) and low occurrence of BCT was particularly evident in the Big Arm of St. Charles Creek. Further research evaluating the abiotic and biotic factors associated with low distribution and abundance of BCT in St. Charles Creek would benefit the entire population. Continued efforts in tributaries to Bear Lake (i.e., habitat restoration, removal of nonnative fishes) should be a management priority in the future. Continuing to screen irrigation diversions and monitoring their effectiveness is especially important, particularly since most BCT outmigrated during periods of irrigation and diversions were negatively related to BCT outmigration.

Chapter 3 provided a comprehensive understanding of BCT population dynamics and harvest management in Bear Lake. My findings highlighted interesting variations in the age and length structure of hatchery and wild BCT. Both groups of fish grew relatively fast in their first few years, declining slightly with age. Bonneville Cutthroat Trout in Bear Lake are long lived and grow to large sizes when compared to other Cutthroat Trout populations. I evaluated a two daily bag limit and a six daily bag limit for wild BCT to evaluate effects of exploitation. Despite differences observed in the two groups, the estimated exploitation rate for current harvest regulations (i.e., two hatchery fish daily bag limit) would be a sustainable level for wild fish. If a six fish daily limit was adopted, recruitment overfishing would likely occur. However, any management actions should be monitored closely and changes in population demographics should be assessed to evaluate effects of exploitation. Environmental (i.e., lake water level, water temperature) and ecological factors (i.e., invasive species, density dependence) that change fish population dynamics are hard to predict and continued monitoring is essential to ensure the persistence of BCT. Collectively, the knowledge gained from my research not only provides insight in BCT in the Bear Lake system, but my work will be useful for managing and conserving BCT in other areas of their distribution.