# Population Dynamics and Harvest Management of the Bonneville Cutthroat Trout Fishery in Bear Lake, Idaho-Utah 

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#### 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, Idaho-Utah, 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 consisted of wild fish; 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 . We 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 O. clarkii in other systems. The current rate of exploitation for hatchery BCT was estimated as 0.27 (i.e., two-fish daily limit). If


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#### Abstract

the limit were changed to a six-fish daily limit, the rate of exploitation would be approximately 0.47 . A yield-perrecruit model evaluating spawning potential ratio indicated that a limit of two wild fish 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 ecologically and recreationally important population.


Rehabilitation of wild Bonneville Cutthroat Trout (BCT) Oncorhynchus clarkii utah has been a focus of fishery management since the late 20th century (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 (Teuscher and Capurso 2007). Over the past century, the distribution and abundance of BCT have 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 (Teuscher and Capurso 2007). The importance of managing BCT for ecological and recreational benefits is typified at Bear Lake, IdahoUtah.

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 relatively 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. spilonotus, 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 $O$. 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; therefore, 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. 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 the 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 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 (S. A. Tolentino, unpublished data). Additionally, the catch per unit effort (CPUE = number of BCT/gill-net hour) increased during the same period. 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). For instance, growth analyses can provide insight on time to achieve important sizes (e.g., "trophy" lengths; Allen and Hightower 2010) and are critical for guiding harvest management decisions. 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). 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 (Kerns and Lombardi-Carlson 2017). Although population trends have been monitored with standardized annual netting in Bear Lake, information on population vital rates is unavailable. Additionally, very little is known about the life history of this unique population of BCT. The objectives of our 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 (Figure 1) to provide estimates of relative abundance and composition (i.e., hatchery or wild) during 2017-2020. Each site was sampled three times per year: lake prestratification (spring), stratification (summer), and poststratification (fall). Monofilament experimental gill nets were 48.7 m long and 1.8 m deep and had 10 panels with 12.7-, 19.1-, 25.4-, 38.1- and $50.8-\mathrm{mm}$ 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 h , all fishes were removed from nets and sacrificed. Each net was reset for an additional 24 h , resulting in a total set time of 48 h per location. We 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 BCT in Strawberry Reservoir, Utah. The monofilament gill nets were 53.3 m long and 6.1 m deep and had seven panels with 12.7-, 19.1-, 25.4-, 38.1-, $50.8-, 63.5$-, and $76.2-\mathrm{mm}$ bar-measure mesh. Nets were initially set at randomly selected sites, but catch rates were very low. As such, subsequent samples were 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 TL (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, Illinois) 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 (Media Cybernetics, Rockville, Maryland) using standard methodologies for annulus identification (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 because notable differences were not observed across years or gear types. Because not all fish were aged, an age-length key was used to estimate the age distribution for all BCT sampled by UDWR from 2017 to 2020 (Isermann and Knight 2005; Quist et al. 2012). Length structure was summarized using lengthfrequency histograms and further evaluated using proportional size distribution (PSD; Gabelhouse 1984; Neumann et al. 2012). We 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 ( $\leq 200$ mm ), multiplied by 100 . Length categories for BCT included quality ( $\mathrm{Q} ; 350 \mathrm{~mm}$ ), preferred ( $\mathrm{P} ; 450 \mathrm{~mm}$ ), memorable ( $\mathrm{M} ; 600 \mathrm{~mm}$ ), and trophy ( $\mathrm{T} ; 750 \mathrm{~mm}$ ). Based on evaluating weighted catch curves and age-specific catch, age-4 and older fish were considered fully recruited


FIGURE 1. Map of Bear Lake, Idaho-Utah, including the three main tributaries. The hollow circles represent gill netting locations sampled in 20172020.
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). We used age 4 because BCT appeared to be recruited to the sampling gear at that age for hatchery fish. Although the frequency of wild age-4 BCT in the sample was less than the frequency of age- 5 fish, age- 4 wild fish were likely equally susceptible to the sampling gear given that their length was similar to the length of age-4 hatchery BCT. Nevertheless, a weighted catch curve was also used to estimate total annual mortality rates for age- 5 and older fish. Total annual mortality estimates using age-5 and older BCT were similar ( $\sim 4 \%$ higher for both wild and hatchery fish) to estimates using age-4 and older fish. Therefore, we assumed that all age-4 BCT were fully recruited to the gear for the purpose of this study. Differences in length and age structure among wild and hatchery fish were evaluated using a Kruskal-Wallis test, followed by pairwise Wilcoxon rank-sum tests (Higgins 2004). A type I error rate of 0.05 was used for statistical tests.

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 mean lengths at age at capture, growth rates of BCT were also described using von Bertalanffy growth models:

$$
L_{t}=L_{\infty}\left[1-e^{-k\left(t-t_{0}\right)}\right]
$$

where $L_{t}(\mathrm{~mm})$ is the length at time $t$ (years), $L_{\infty}$ 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 Bever-ton-Holt yield-per-recruit model (Beverton and Holt 1957; Ricker 1975; Goodyear 1993). The SPR model incorporates a variety of parameter estimates derived from fish populations, including total annual mortality, von Bertalanffy growth model parameters, conditional fishing mortality ( $c f$ ), conditional natural mortality ( cm ), maximum fish age, and length-weight and fecundity-length equation parameters. 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 is less than 0.20 (i.e., $80 \%$ reduction in egg production), then recruitment overfishing may occur and result in a population decline. We constructed models using the Fishery Analysis and Modeling Simulator (Slipke and Maceina 2014). All parameters used in the model were derived from the wild population of BCT except for fecundity estimates (Table 1). We were unable to directly estimate fecundity of BCT in Bear Lake due to low sample size for suitable fish. Therefore, we used the equation (fecundity $=0.0026 \times \mathrm{TL}^{2.2255}$ ) for Yellowstone Cutthroat Trout O. clarkii bouvieri in Idaho from Meyer et al. (2003). The sex ratio of the wild population was specified as 0.5 because the observed sex ratio did not differ significantly ( 0.53 female; $95 \%$ CI: $0.48-0.58$ ). Using creel data collected from Bear Lake by UDWR, we estimated that $95 \%$ of harvested BCT were $\geq 400 \mathrm{~mm}$; therefore, we used 400 mm as the minimum length harvested by anglers. Currently, there is no minimum length limit for BCT in Bear Lake. Parameter estimates from the von Bertalanffy growth model, estimates from the lengthweight relationship (i.e., $\log _{10}[$ weight $]-4.793+2.888 \times$ $\log _{10}[$ 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, we were able to estimate fishing mortality ( $F$ ) and exploitation ( $\mu$ ) 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-fish daily bag limit) was calculated. We assumed that $\mu$ of wild fish would be equal to $\mu$ of hatchery fish. Using creel data from 2010 and 2015 in Bear Lake, we estimated the exploitation rate of a six-fish daily bag limit by dividing the reported total sum 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 $\mu$ 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 model as 0.24 (i.e., $A$ for the fish that do not experience harvest). Conditional fishing mortality ( $c f$ ) was varied in the model from 0.00 to 0.90 in increments of 0.05 . For each model iteration, we used 1,000 individuals as the number of recruits. We modeled a "worst-case" scenario in which $100 \%$ of fish harvested would be of wild origin. Two different harvest scenarios were evaluated using the yield-per-recruit model. More specifically, we evaluated SPR under two- and six-

TABLE 1. Parameters used in a spawning potential ratio yield-perrecruit model for the wild Bonneville Cutthroat Trout population sampled from Bear Lake, Idaho-Utah, in 2017-2020 via gill nets $\left(L_{\infty}=\right.$ mean asymptotic length; $k=$ growth coefficient; $t_{0}=$ theoretical age when length is zero).

| Parameter | Value |
| :---: | :---: |
| Von Bertalanffy growth coefficients | $\begin{aligned} & L_{\infty}=684 \mathrm{~mm} \\ & k=0.180 ; t_{0}=0.15 \end{aligned}$ |
| Maximum age | 12 years |
| Conditional natural mortality | 0.24 |
| Conditional fishing mortality | 0.0-0.90 |
| $\log _{10}$ (weight) $\log _{10}$ (length) coefficients | $a=-4.793 ; b=2.888$ |
| Age at sexual maturation | 5 years |
| Fecundity-to-length relation | $-3,583.90+12.54$ (length) |
| Percentage of fish that are females | 50\% for all age-classes |
| Percentage of females spawning annually | $15 \%$ for age $5 ; 70 \%$ for age 6 ; $94 \%$ for age $7 ; 100 \%$ for age 8 to age 12 |
| Minimum length limit | 400 mm TL |
| Number of recruits | 1,000 fish |

fish daily bag limits for wild BCT. A two-fish limit was evaluated because it would maintain the current bag limit but allow inclusion of wild BCT in the harvest. We also evaluated a six-fish limit as this is consistent with IDFG's general Cutthroat Trout $O$. clarkii bag limit in southeast Idaho.

## RESULTS

During the spring, summer, and fall months of 20172020, 807 individual BCT were captured in gill nets in Bear Lake. Average BCT catch rate in gill nets was 0.11 fish/h ( $\mathrm{SE}=0.01$ ), and the proportion of hatchery fish sampled (0.47) was less than the proportion of wild fish (0.53). Total lengths of fish were significantly different between hatchery and wild fish ( $P<0.05$ ). In general, sampled wild BCT were larger than hatchery fish and varied in length from 190 to 702 mm (Figure 2; mean $\pm$ SE: 463 $\pm 5 \mathrm{~mm}$ ). Hatchery BCT varied in length from 169 to 640 $\mathrm{mm}(400 \pm 4 \mathrm{~mm})$. 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 2). Similarly, most of the stock-length wild BCT were also quality length; wild preferred and memorable-length BCT were


FIGURE 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) and memorable (PSD-M) lengths. No trophylength (PSD-T) fish were sampled.
more common than for hatchery fish. No trophy-length wild or hatchery BCT were sampled.

Estimated age structure was significantly different between hatchery and wild fish $(P<0.05)$. Age of wild BCT varied from 2 to 12 years, and wild fish were generally older ( $6.5 \pm 0.1$ years) than hatchery fish ( $5.0 \pm 0.1$ years), whose ages varied from 2 to 11 years (Figure 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 fish than for hatchery fish. Total annual mortality of age-4 to age-11 hatchery

BCT (mean $\pm$ SE: $0.47 \pm 0.05$ ) was higher than for wild fish ( $0.24 \pm 0.06$; Figure 3). Growth was similar between hatchery and wild fish except that $L_{\infty}$ was lower for hatchery fish ( $549 \pm 22.0 \mathrm{~mm}$ ) than for wild fish ( $684 \pm$ 27.1 mm ; Figure 4). Exploitation of hatchery BCT under current regulations was estimated as 0.27 . If the daily bag limit allowed harvest of six wild fish, $\mu$ 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. Spawning potential ratio of BCT declined as rates of exploitation increased (Figure 5). At


FIGURE 3. Age structure of Bonneville Cutthroat Trout sampled from Bear Lake, Idaho-Utah, in 2017-2020 ( $A=$ total annual mortality $)$.
current levels of $\mu(0.27)$ and $\mathrm{cm}(0.24)$, SPR was above the $0.20-0.30$ threshold $(\sim 0.35)$. If a higher SPR of 0.30 is considered, exploitation would likely have to exceed 0.35 to result in recruitment overfishing and may lead to a population decline. If a less conservative SPR of 0.20 is adopted, $\mu$ could increase to about 0.45 before there are concerns for overfishing.

## DISCUSSION

The wild population of BCT in Bear Lake has increased in the past decade, but population demographics and the potential effects of angler exploitation have not been evaluated. Our study is the first of its kind to provide information on the population rate functions of adfluvial BCT and assess the potential effects of harvest on a wild population of BCT. Adfluvial populations of trout are often highly susceptible to environmental perturbations and are of conservation concern (Tennant et al. 2016; 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, we 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. We further assessed the populationlevel 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 that of 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 growth 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 $8-9$ years and achieve a maximum length of about 600 mm . However, adfluvial Yellowstone Cutthroat Trout in Henrys Lake, Idaho, had a maximum length of 650 mm and a 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 2 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 that


FIGURE4. Von Bertalanffy growth model fit to mean length at age-at-capture for Bonneville Cutthroat Trout sampled from Bear Lake, IdahoUtah, in 2017-2020 ( $L_{i n f}=$ mean asymptotic length $)$.

Westslope Cutthroat Trout $O$. 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 size at maturity of Yellowstone Cutthroat Trout in Yellowstone Lake (Syslo 2015). All fish were mature at approximately 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 3-5 (Downs et al. 1997). We were unable to directly estimate fecundity of BCT in Bear Lake and used an equation for


FIGURE 5. Spawning potential ratio (SPR) 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.
fecundity of Yellowstone Cutthroat Trout in the South Fork Snake River to estimate BCT fecundity. Using the Meyer et al. (2003) equation, we estimated mean fecundity of Bear Lake BCT at 2,989 eggs/female. Additionally, we 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 than the equation derived from the South Fork Snake River. Therefore, we 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 are likely a function of the fishery on hatchery fish. Although exploitation rates vary, our estimate of exploitation is within the distribution of values reported for western trout fisheries. Schill et al. (2007) reported exploitation rates less than $1 \%$ for Columbia River Redband Trout $O$. mykiss gairdneri in eight Idaho desert streams. However, exploitation rates in more accessible and popular Rainbow Trout fisheries in Idaho varied from $2 \%$ to $40 \%$ (Schill and Meyer 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., $\sim 24-47 \%$ ) were similar to estimates for other Cutthroat Trout populations. Simmons et al. (2020) reported that total annual mortality of Lahontan Cutthroat Trout O. 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 occurred 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 et al. 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 et al. 2002). A critical SPR level of $20 \%$ was used for Silver Carp Hypophthalmichthys molitrix to cause recruitment overfishing in the Midwestern United States (Seibert 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. 2009). 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, we also developed a deterministic, female-based Leslie matrix (results not shown here) 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 (i.e., sustainable harvest of wild BCT at a two-fish limit), but we opted to use the Beverton-Holt model for its simplicity and clarity. However, additional monitoring is important to guide future management efforts in the event that compensatory responses emerge with harvest of wild BCT.

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. The results from population models indicate that wild BCT in Bear Lake can sustain the current level of exploitation observed for hatchery fish. However, it is important to note that we made several assumptions in our analysis. 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 an assessment would not only allow managers to refine population information associated with BCT but would 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 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, future studies could evaluate the potential for a length-based harvest regulation if there is concern of recruitment overfishing in response to harvest of wild BCT (Beard et al. 2003; Isermann and Paukert 2010). Changes in harvest regulations could also influence angler behavior (Beard et al. 2003). Allowing harvest of wild BCT in Bear Lake might attract additional angling effort and thereby increase exploitation. Furthermore, because wild BCT did not recruit to the gear in
annual gill netting surveys until fish were age 4 and older, effects of harvest on recruitment of BCT might not be detected for 4 years or more. Again, detailed monitoring will help address these and other issues that may emerge following changes in management. This study serves as a baseline of BCT population dynamics for future monitoring and can be used to help guide additional 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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