Article

Population Dynamics of Yellowstone Cutthroat Trout in Henrys Lake, Idaho

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Abstract

Yellowstone Cutthroat Trout (YCT) *Oncorhynchus clarkii bouvieri* is a species with significant ecological and recreational value. In many YCT fisheries, managers are tasked with balancing angler expectations and fish conservation. Henrys Lake supports a popular trophy trout fishery, but the increase of nonnative Utah Chub *Gila atraria* has caused concern for YCT. We summarized long-term trends in abundance, length structure, body condition, and growth of YCT to evaluate the effect of Utah Chub. Additionally, we investigated abiotic and biotic factors influencing YCT. We examined archived hard structures to provide a comprehensive evaluation of changes in age and growth of YCT in the system. We used stocking records and catch rates of Utah Chub and trout in Henrys Lake as covariates to explain changes in YCT catch rates and growth. Catch rates varied from 1.5 to 15.4 YCT per net night during the 2002 to 2020 sampling period, but we did not identify consistent patterns. Length structure was consistently dominated by stock- to quality-length fish, and we captured few fish >600 mm in total length. Relative weight of YCT was decreased from a mean ± standard deviation (SD) of 115.9 ± 16.5 in 2004 to 93.2 ± 8.2 in 2020. The age of YCT varied between 1 and 11 years; fish that we captured during 2010 to 2020 were the oldest. The majority of fish that we sampled were age 4 and younger. Total annual mortality of age-2 and older YCT was higher than other Cutthroat Trout populations (i.e., 0.70 during 2002 to 2010 and 0.60 during 2011 to 2020). Based on regression models, we identified positive relationships between catch rates of YCT, Brook Trout *Salvelinus fontinalis,* and Rainbow Trout *Oncorhynchus mykiss* × YCT hybrid trout. We observed negative relationships between growth of YCT and abundance of Utah Chub and Brook Trout. Although we identified negative relationships, YCT growth in recent decades is as fast as or faster than earlier time periods. Results from this research suggest that major changes in YCT population dynamics are not evident over the last 20 years. This study provides insight into the factors influencing an adfluvial trout population. In particular, results from this research may be useful for managers of systems where Utah Chub have been introduced.

Keywords: population dynamics; Yellowstone Cutthroat Trout; adfluvial trout; Henrys Lake; growth

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Introduction

The introduction of nonnative species is a primary threat to freshwater ecosystems (Dudgeon et al. 2005). Species have been introduced across the globe for a variety of purposes, including aquaculture, aquaria, and sport fishing opportunity (Rahel 2000; Copp et al. 2005). Many of these introductions have been intentional, but accidental introductions through ballast water and illegal stockings have also occurred (Rahel 2000). Although society has benefited from some introductions, many populations of native fishes have suffered from negative interactions with nonnative species (Rahel 2002; Gozlan 2008).

In many systems, the effect of introduced species is poorly understood, which presents concern for resource managers. Utah Chub *Gila atraria* is one species that has spread outside its native distribution and become a detriment to native salmonid populations (Hazzard 1935; Davis 1940; Winters and Budy 2015). Utah Chub is native to the Lake Bonneville basin in Utah, Idaho, and Nevada and the Snake River drainage of Idaho upstream of Shoshone Falls and downstream of Mesa Falls (Sigler and Sigler 1996). Utah Chub tolerates a wide variety of temperatures (i.e., 15.6–31.1°C) and is common in systems with dense aquatic vegetation. Utah Chub is omnivorous and shifts its diet in response to prey availability (Graham 1961; Sigler and Sigler 1996). The wide variety of habitat and food tolerances has likely contributed to Utah Chub establishment outside its native distribution.

Utah Chub is frequently considered a nuisance species and is not targeted by anglers (Graham 1961). In addition, Utah Chub often compete with popular sport fishes (Davis 1940; Sigler and Sigler 1996; Teuscher and Luecke 1996). The diet of Utah Chub is similar to salmonids, and diet overlap has been documented in many systems (Schneidervin and Hubert 1987; Teuscher and Luecke 1996; Winters and Budy 2015). However, Winters et al. (2017) reported that adult Bonneville Cutthroat Trout *Oncorhynchus clarkii utah* consumed Utah Chub. Although they may be a prey resource in some systems, high abundance of Utah Chub is associated with declines in salmonid growth (Teuscher and Luecke 1996; Winters and Budy 2015). In Fish Lake, Utah, a decline in trout abundance was associated with competition with Utah Chub for prey resources (Hazzard 1935; Davis 1940).

Nonnative Utah Chub is a concern in Henrys Lake, Idaho. Utah Chub was first detected in Henrys Lake in 1993 and has since become abundant (Gamblin et al. 2001; Heckel et al. 2020). For example, catch rates of Utah Chub increased 16-fold from 2002 to 2018 (Heckel et al. 2020). Henrys Lake is a shallow lake located in eastern Idaho near the Idaho–Montana border that is managed for trophy Rainbow Trout *Oncorhynchus mykiss* × Yellowstone Cutthroat Trout (YCT) *O. c. bouvieri* hybrids, YCT, and Brook Trout *Salvelinus fontinalis* (Figure 1; Campbell et al. 2002). Conserving native YCT is also a high priority for resource managers. The Idaho Department of Fish and Game (IDFG) stocks sterile Rainbow Trout × YCT hybrids and Brook Trout in an attempt to balance these management objectives in Henrys Lake. Yellowstone Cutthroat Trout is considered particularly vulnerable to the negative effects of nonnative species (Gresswell 2011; Al-Chokhachy et al. 2018; Budy et al. 2019). In 2011, genetically pure populations of YCT occupied only 28% of their historical distribution (Gresswell 2011). As a result, YCT is a species of high conservation concern by natural resource agencies. Yellowstone Cutthroat Trout maintain high ecological, cultural, and economic value, so minimizing the negative effects of nonnative species is a top priority for natural resource agencies.

Despite the popularity of Cutthroat Trout as a sport fish, numerous knowledge gaps remain. In particular, little is known about the population dynamics of adfluvial Cutthroat Trout, which often complicates their conservation and management. Henrys Lake supports

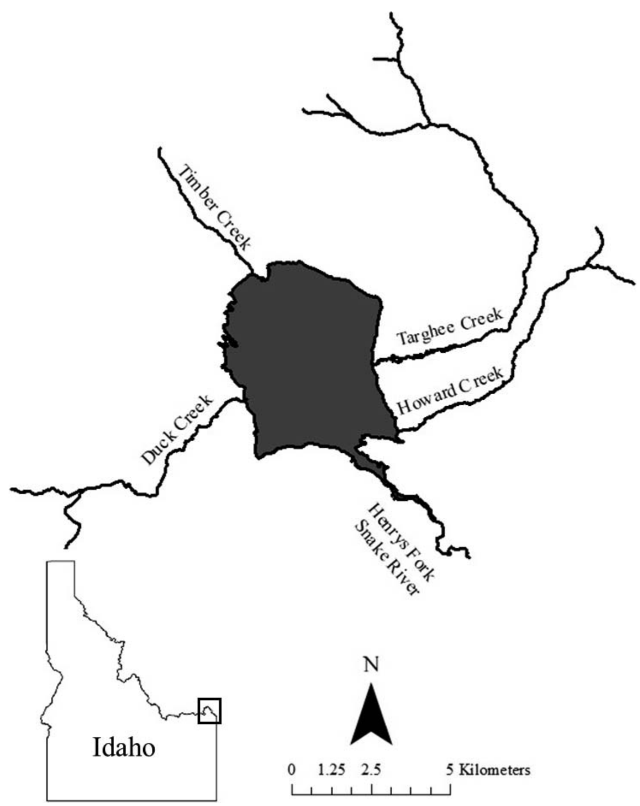

Figure 1. Map of Henrys Lake, Idaho (shaded), and major tributaries. Henrys Lake is the study area for the evaluation of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* population dynamics 1970s to 2020.

Table 1. Sampling method, hard structures that were collected for age and growth analysis, and number of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* aged from Henrys Lake, Idaho (1971–2020).

Decade	Sampling method	Structure	Number aged
1971–1980	Creel	Scales	37
1981–1990	Creel, trap net, purse seine	Scales	154
1991–2000	Gill net	Scales	38
2001–2010	Gill net	Otoliths	1,193
2011–2020	Gill net	Otoliths	1,832

adfluvial YCT and provides a unique opportunity to learn more about adfluvial Cutthroat Trout. Historically robust, YCT face several threats, including nonnative Utah Chub. The IDFG reported increasing catch rates of Utah Chub in their annual gill net surveys in Henrys Lake over the last two decades (2000–2020; High et al. 2015; Flinders et al. 2016a; Heckel et al. 2020). Patterns and potential response of YCT have not been thoroughly investigated. Understanding the population dynamics of both nonnative Utah Chub and native YCT in Henrys Lake is important, particularly as the environment shifts to less favorable conditions for trout (i.e., climate change and warming temperatures).

We sought to describe long-term trends in abundance, length structure, body condition, age structure, and growth of YCT. Specifically, we strove to evaluate potential effects of Utah Chub on YCT and identify abiotic and biotic factors influencing the population dynamics of YCT in Henrys Lake. Additionally, we modeled relative abundance and growth to identify factors related to abundance and growth through time. We predicted that Utah Chub abundance and warm temperatures would be negatively related to catch rates and growth of YCT. Additionally, we expected that growth of YCT would be influenced by density-dependent characteristics (e.g., abundance of trout and stocking rates).

Methods

Study area

Henrys Lake is a shallow eutrophic lake located in eastern Idaho (Figure 1). Although Henrys Lake is relatively shallow (mean depth = 4 m; Flinders et al. 2016a), it supports a renowned trophy trout fishery for YCT, Rainbow Trout × YCT hybrids, and Brook Trout (Campbell et al. 2002; Roth et al. 2020). Since the 1970s, an extensive hatchery supplementation program has primarily maintained the trout fishery (Rohrer and Thorgaard 1986; Campbell et al. 2002).

Data collection and summarization

We compiled historical fishery data from IDFG's annual population surveys (i.e., 1970–2020; Data S1, *Supplemental Material*). Surveys provided information on the number of fish sampled, sampling effort, and total length (TL; in millimeters) of sampled fish. Beginning in 2004, we recorded weight measurements (in grams) to monitor body condition. We also collected hard structures (i.e., scales and sagittal otoliths) during population surveys (Data S2, *Supplemental Material*). We removed scales from all YCT sampled before 2002. After 2002, we collected otoliths from all YCT sampled. The body location of where scales were removed for historical samples is unknown but was likely from the area just posterior to the pectoral fin. During processing, we subsampled hard structures from 10 fish per centimeter length group for each year. We pressed scales onto acetate slides and viewed them with a dissecting scope (McInerny 2017). We mounted sagittal otoliths in epoxy and cut a thin section along the dorsoventral plane using an IsoMet Low Speed saw (Buehler Inc., Lake Bluff, IL; Koch et al. 2009; Long and Grabowski 2017). A single reader without knowledge of fish length estimated ages. The reader had experience ageing fish with sagittal otoliths. In addition, we used a subsample of known-age YCT from Henrys Lake for training. We measured incremental growth with ImagePro software (Media Cybernetics, Inc., Rockville, MD).

We quantified changes in catch rates, length structure, and relative weight from 2002 to 2020. Before 2002, we used a variety of gear types for population assessments on Henrys Lake, including trap nets, a purse seine, and various gill nets (Table 1). In 2002, Idaho Department of Fish and Game standardized gill net surveys. We limited the long-term trends in catch rates, length structure, and relative weight to the period between 2002 and 2020 to avoid the influence of biases associated with nonstandardized sampling before 2002. We calculated catch rates for YCT as catch per net night of all fish and by standard length category, that is, stock (200–349 mm TL), quality (350–449 mm TL), preferred (450–599 mm TL), memorable (600–749 mm TL), and trophy (≥750 mm TL). We calculated total catch rates for Brook Trout, hybrid trout, and Utah Chub for all fish by species and summarized length structure using proportional size distribution (PSD; Neumann et al. 2012). We calculated relative weight (W_r) for all fish and by length category to evaluate body condition (Kruse and Hubert 1997; Neumann et al. 2012), and we calculated standard weight (W_s) as

$$\log_{10}(W_s) = a' + b \times \log_{10}(L) \leftarrow$$

where the intercept (a') is –5.192, the slope (b) is 3.086, and L is TL (Neumann et al. 2012).

We developed an age-length key and used it to estimate the age structure of YCT from 2002 to 2020 from the subsampled YCT ($n = 3{,}025$; Quist et al. 2012). We considered age-2 and older fish fully recruited to the gear based on age-specific catches. We used a weighted catch curve to calculate total annual mortality for age-2 to age-11 YCT (Smith et al. 2012) and summarized total annual mortality estimates by decade (i.e., 2002 to 2010 and 2011 to 2020). We estimated back-calculated length at age by measuring the distance from the focus of the scale or nucleus of the otolith to each annulus (Quist et al. 2012). For scales, we estimated back-calculated lengths with the Fraser–Lee method

$$L_i = \left(\frac{L_c - a}{S_c}\right) S_i + a$$

where L_i is the back-calculated length of the fish when the ith annulus was formed, L_c is the length of the fish at capture, S_c is the radius of the scale at capture, S_i is the radius of the scale at the ith annulus, and a is the intercept of the regression of fish length at capture on scale radius at capture. We estimated back-calculated lengths for otoliths with the Dahl–Lea method

$$L_i = L_c \left(\frac{S_i}{S_c}\right)$$

where L_i is the back-calculated length of the fish when the ith annulus was formed, L_c is the length of the fish at capture, S_c is the radius of the otolith at capture, and S_i is the radius of the otolith at the ith annulus. We summarized back-calculated lengths at ages 2 to 4 by decade and limited growth comparisons to ages 2 to 4 because of concerns with age estimates from scales. Ages are frequently underestimated from scales due to difficulty identifying the first annulus, crowding on the edge structure, and (or) resorption (Hoxmeier et al. 2001; Kaeding and Koel 2011; McInerny 2017). Comparisons between YCT scales and sectioned otoliths from fish in Henrys Lake indicate that back-calculated lengths of scales and otoliths are similar from age 2 to 5 (D.K.M., unpublished data). Summarizing back-calculated lengths by decade helped mitigate errors associated with age estimates from scales and allowed for broad comparison over a longer time period.

We also compiled historical stocking and environmental data. Stocking records included species, date of stocking, number stocked, and average length at stocking (Data S3, *Supplemental Material*). Long-term water temperature data do not exist; therefore, we used air temperature as a surrogate for water temperature during open water periods (Data S4, *Supplemental Material*). We obtained air temperature (°C) and snow-to-water equivalent (cm) data from Natural Resources Conservation Service SNOTEL Site 546 in Island Park, Idaho (Data S5, *Supplemental Material*). We calculated a variety of temperature variables (e.g., average, minimum, and maximum) annually for the growing season (1 May to 31 October) and summer (20 June to 22 September). We downloaded lake volume (m^3) information from the U.S. Geological Survey gage on the dam (Data S6, *Supplemental Material*; USGS 2020).

Data analysis

We further analyzed catch rates and growth of YCT with regression analysis to evaluate relationships with environmental and biological characteristics. Although we evaluated PSD and relative weight (W_r), length and weight data are often biased by a variety of factors, including gear type and time of year (e.g., spawning; Neumann et al. 2012). As such, we did not develop regression models for PSD and W_r. Covariates in models for catch rates and growth of YCT included air temperature, snow-to-water equivalent, reservoir volume, catch rates for each species, and stocking rates for each species. We also included time lags for stocking variables. We evaluated multicollinearity with Spearman's correlation coefficient (Sokal and Rohlf 2001). If two covariates were significantly correlated (Spearman's $r \geq |0.70|$), we retained the most ecologically relevant variable for further analysis. For example, maximum air temperature during the growing season and annual maximum air temperature were highly correlated. We deemed maximum air temperature during the growing season as more ecologically relevant, so we retained it for candidate models.

We created regression models for catch rates with a Poisson distribution using the glm function in the R statistical program (R Core Team 2018). Total count was the response variable, and we used an offset variable for effort. We evaluated growth with mixed effects models (Weisberg 1993; Weisberg et al. 2010; Watkins et al. 2017) and estimated growth coefficients with a repeated-measures mixed-effects linear model that evaluated the effects of age and year on annual growth increments (Weisberg et al. 2010). We treated year and individual fish as random effects and age as a fixed effect. Due to concerns with scales, we only calculated growth coefficients for years during which we collected otoliths (i.e., 2002 to 2020). We created linear regression models using the growth coefficients as the response variable and air temperature, snow-to-water equivalent, reservoir volume, catch rates for each species, and stocking rates for each species as explanatory variables.

We evaluated regression models for catch rates for overdispersion. We calculated the dispersion parameter ($\hat{c}$) by dividing Pearson's residual deviance by the residual degrees of freedom (Burnham and Anderson 2002). If the dispersion parameter was greater than one, we considered the model overdispersed. We ranked models that were not overdispersed with Akaike's Information Criterion adjusted for small sample size (AIC_c). We used quasi-AIC_c to evaluate models that were overdispersed, and we added an additional parameter to K. We included null models during model evaluation. The top model had the lowest AIC_c or $QAIC_c$ score, and we considered models within two AIC_c or $QAIC_c$ points in the top models. We further evaluated model fit with the coefficient of determination (R^2; Sokal and Rohlf 2001). For overdispersed models, we used McFadden's pseudo R^2 to evaluate model fit and calculated it as one minus

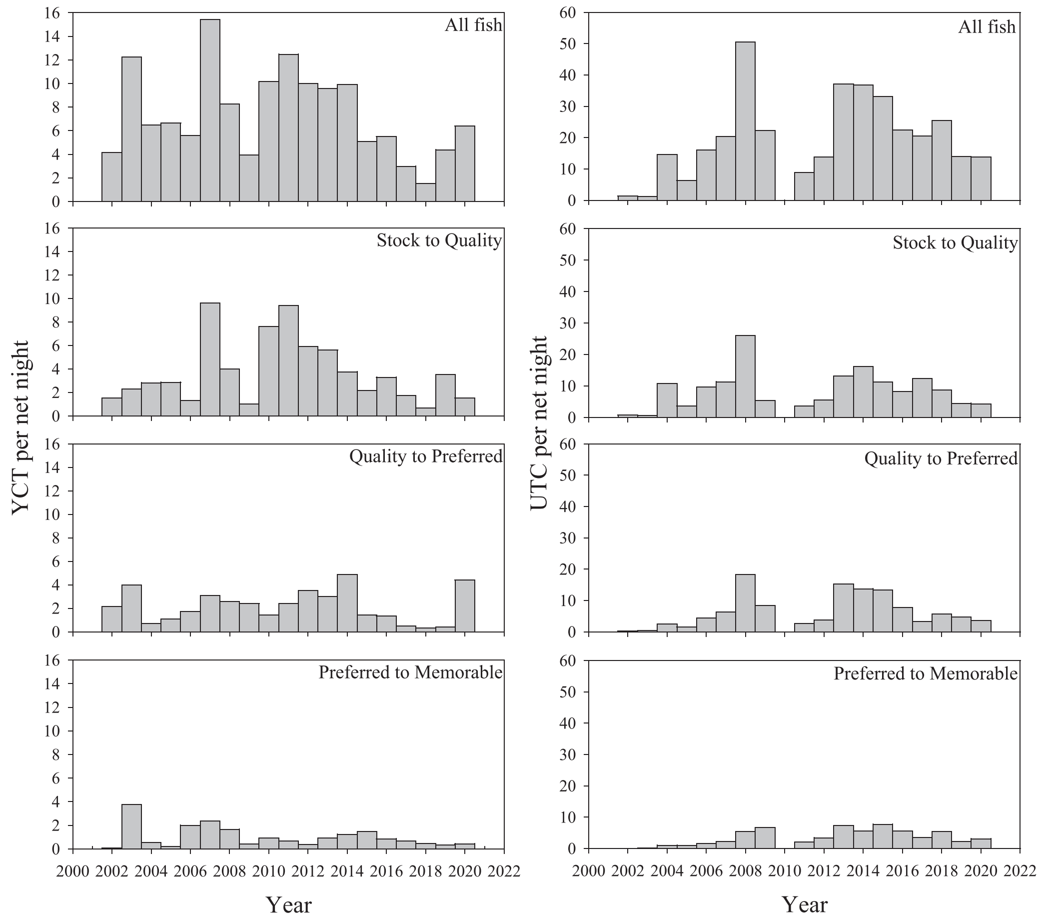

Figure 2. Catch per unit of effort (fish/net night) for Yellowstone Cutthroat Trout (YCT) *Oncorhynchus clarkii bouvieri* and Utah Chub (UTC) *Gila atraria* in Henrys Lake, Idaho, from annual gill net surveys (2002–2020). Length categories for YCT include stock to quality (200 to 349 mm), quality to preferred (350 to 449 mm), preferred to memorable (450 to 599 mm), and memorable to trophy (600 to 749 mm). We captured no trophy-length fish and few memorable- to trophy-length YCT ($n = 5{,}524$). Length categories for UTC include stock to quality (100 to 199 mm), quality to preferred (200 to 249 mm), preferred to memorable (250 to 299 mm), and memorable to trophy (300 to 379 mm).

the ratio of the log likelihood of a model with parameters and the intercept-only model (McFadden 1974). We considered models with a McFadden's pseudo R^2 value of 0.20–0.40 excellent models, but models with R^2 values as low as 0.10 have good fit (McFadden 1974; Hosmer and Lemshow 1989; Klein et al. 2015).

Results

Catch per unit of effort from 2002 to 2020 was variable across years and averaged 7.4 ± 3.6 YCT per net night (mean ± SD) and 19.9 ± 13.0 Utah Chub per net night (Figure 2). Catch rates of YCT peaked in 2007 at 15.4 YCT per net night. Utah Chub catch rates peaked in 2008 with 50.5 Utah Chub per net night. YCT catch rates declined consistently from 2011 to 2018. Catch was primarily comprised of stock–quality- and quality–preferred-length fish. The relative abundance of preferred–memorable-length YCT also varied through time and has generally declined since 2015. Length structure of YCT in Henrys Lake varied through time (Figure 3). We sampled no trophy-length and few memorable-length YCT from 2002 to 2020. Relative weights varied across years and have decreased from an average of 116 ± 16.5 in 2004 to 93 ± 8.2 in 2020 (Figure 4). Relative weights were similar across length categories each year except for preferred–memorable-length YCT, which had slightly lower relative weights than the other length categories.

In total, 3,254 YCT scales and otoliths were aged (Table 1). Yellowstone Cutthroat Trout TL varied from 105 to 650 mm (mean ± SD; 356.6 ± 91.1 mm) and in age from 1 to 11 years (2.7 ± 1.1 years). Age structure varied through time and was dominated by age-4 and younger fish (Figure 5; Table S1, *Supplemental Material*). Growth of age-2 to age-4 fish was similar across decades, with slightly higher mean back-calculated length in the two most recent decades (Figure 6). Using just otoliths from fish that we collected after 2002, age-1 to age-6 YCT grew fastest during 2002 to 2010 (Figure 7). Age-7 and older YCT grew faster from 2011 to 2020 than during the prior decade. We estimated total annual mortality for age-2 and older YCT at 0.70 during 2002 to 2010 and 0.60 during 2011 to 2020.

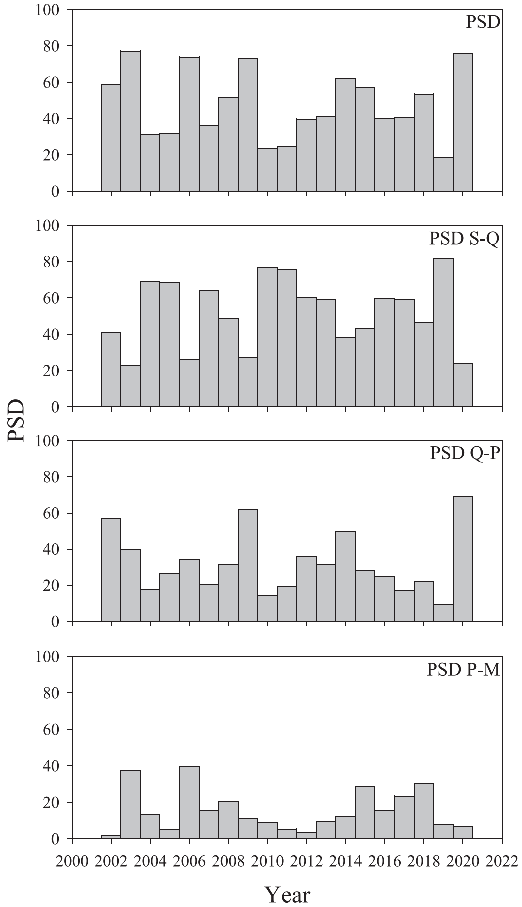

Figure 3. Proportional size distributions (PSD) for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho, from annual gill net surveys (2002–2020). Length categories include stock to quality (S–Q; 200 to 349 mm), quality to preferred (Q–P; 350 to 449 mm), and preferred to memorable (P–M; 450 to 559 mm).

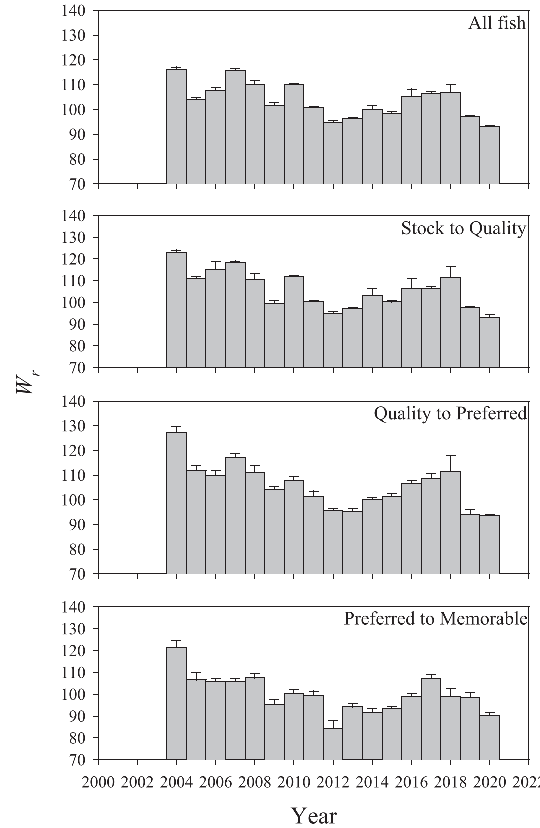

Figure 4. Relative weight (W_r) for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho, from annual gill net surveys (2002–2020). We calculated relative weight for each standard length category. Length categories include stock to quality (200 to 349 mm), quality to preferred (350 to 449 mm), preferred to memorable (450 to 599 mm), and memorable to trophy (600 to 749 mm). Error bars represent standard error.

We further analyzed catch rates and growth with regression modeling. We modeled catch rates by standard-length category, but top models did not provide additional insight beyond those for total YCT abundance. Regression modeling indicated positive relationships between abundance of YCT and the abundance of Brook Trout and hybrid trout (Table 2; Table S2, *Supplemental Material*). However, the null model was also in the top set of models for catch rates of YCT. Growth of YCT was negatively related to catch rates of Brook Trout, Utah Chub, and all trout and positively associated with YCT stocking rates and minimum air temperature during the growing season (Table 3; Table S2, *Supplemental Material*). Brook Trout and Utah Chub catch rates were in three of the top four models for growth of YCT.

Discussion

Cutthroat Trout are declining across their distribution due to negative interactions with nonnative species and habitat degradation (Young 1995; Gresswell 2011; Budy et al. 2019). Despite the ecological and economic importance of Cutthroat Trout, limited information exists on the ecology of adfluvial Cutthroat Trout populations. The lack of information on adfluvial trout complicates comparisons between populations. Our research is a comprehensive analysis of population dynamics of an adfluvial YCT population. Yellowstone Cutthroat Trout are abundant in rivers and streams but are typically much smaller than lacustrine YCT. For example, YCT sampled from lotic populations rarely exceed 400 mm in TL, and few exceed 250 mm in TL (Thurow et al. 1988; Meyer et al. 2003). In contrast, adfluvial populations of Cutthroat Trout often contain fish over 600 mm in TL (Varley and Gresswell 1988; Kaeding and Koel 2011; Heller 2021). Maximum TL of YCT collected from Henrys Lake is comparable to other adfluvial populations of Cutthroat Trout (Kaeding and Koel 2011; Heller 2021).

Yellowstone Cutthroat Trout in Idaho typically live 8 to 9 years (Gresswell 2011). The maximum age of adfluvial Cutthroat Trout can exceed 10 years (Kaeding and Koel 2011; Heller 2021). Similarly, YCT in Henrys Lake had a maximum age of 11 years. The majority of YCT were between ages 2 and 5. Irving (1955) reported that YCT in

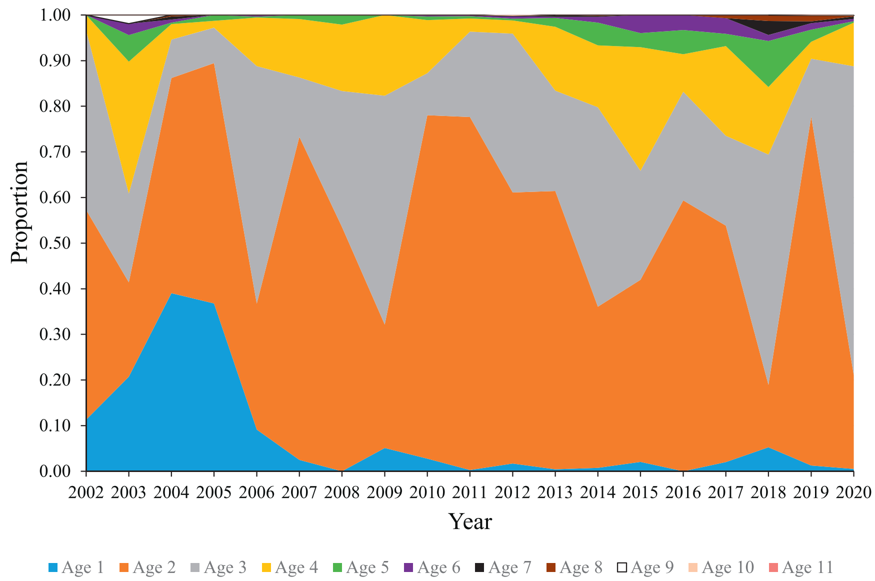

Figure 5. Proportion of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* at each age sampled from Henrys Lake, Idaho, 2002 to 2020.

Henrys Lake live up to 6 years. Although fish may live longer in recent times, the change in apparent longevity is most likely a result of underestimation of age from scales (Kerns and Lombardi-Carson 2017). Yellowstone Cutthroat Trout scales often fail to form a first annulus (Kaeding and Koel 2011), and resorption, regeneration, and crowding make identifying annuli difficult on cycloid scales (Hoxmeier et al. 2001; McInerny 2017). Hard structure comparisons between scales and otoliths of YCT in Henrys Lake suggest that scales underestimate age-at-capture relative to otoliths, particularly in older fish (D.K.M., unpublished data).

Vital rates provide important information on fish populations that are valuable for management decisions. We estimated total annual mortality of age-2 to age-11 YCT in Henrys Lake between 60 and 70%. Mortality rates in Henrys Lake are higher than other lentic Cutthroat Trout populations (e.g., Heller 2021; Simmons et al. 2020). For example, total annual mortality was 47% for Bonneville Cutthroat Trout in Bear Lake, Utah, and 49% for Lahontan Cutthroat Trout *O. c. henshawi* in Summit Lake, Nevada. With regard to growth, YCT in Henrys Lake grow faster than YCT in Yellowstone Lake (Gresswell 2011). Mean back-calculated length at age 2 in Henrys Lake was 259 mm but only 140 mm in Yellowstone Lake. Similar patterns were observed for other ages. Yellowstone Cutthroat Trout in Henrys Lake grow at a rate similar to piscivorous Bonneville Cutthroat Trout in Bear Lake (Heller 2021). For instance, mean back-calculated length at age 3 was 332 mm for YCT in Henrys Lake and 291 mm for Bonneville Cutthroat Trout in Bear Lake. Relatively fast growth of YCT in Henrys Lake could be due to high production of macroinvertebrates or because YCT in the system exhibit some level of piscivory. Although YCT are not typically considered piscivores, we did identify a positive relationship between YCT growth and YCT stocking rates of the same year. One plausible explanation for this relationship is that YCT in Henrys Lake are feeding on the stocked fingerlings. Adfluvial populations of Cutthroat Trout are typically piscivorous (e.g., Bonneville Cutthroat Trout and Lahontan Cutthroat Trout; Gresswell 1988; Winters et al. 2017).

Changes in growth may be associated with interactions with Utah Chub. Unfortunately, regression modeling of YCT growth was limited to the period after we first detected Utah Chub in Henrys Lake. Nevertheless, growth of YCT was negatively related to Utah Chub abundance from 2002 to 2020. The specific mechanism is unknown, but diet overlap and competition between Utah Chub and salmonids is extensively documented in other systems (Schneidervin and Hubert 1987; Teuscher and Luecke 1996; Winters and Budy 2015). For instance, Schofield Reservoir, Utah, is dominated by Utah Chub but also contains several trout species, such as Rainbow Trout, Tiger Trout (Brown Trout *Salmo trutta* × Brook Trout), and Bonneville Cutthroat Trout (Winters and Budy 2015). High diet overlap occurs between all trout species and Utah Chub. Although smaller trout experienced reduced growth as a result of high Utah Chub densities, larger trout relied on Utah Chub for forage (Winters and Budy 2015; Winters et al. 2017). Flinders et al. (2016b) evaluated diet overlap in Henrys Lake to a limited extent, but the results suggested that YCT are not feeding on Utah Chub, and diet overlap was minimal between Utah Chub and YCT. If diet overlap is not occurring at a level that could explain changes in growth, Utah Chub may have an indirect effect (e.g., changes to nutrient dynamics).

Climate change and particularly warming temperatures will likely compound the negative effects of habitat degradation and invasive species on native species (Williams et al. 2009; Budy et al. 2019). Rising temperature is a concern for aquatic systems, especially for

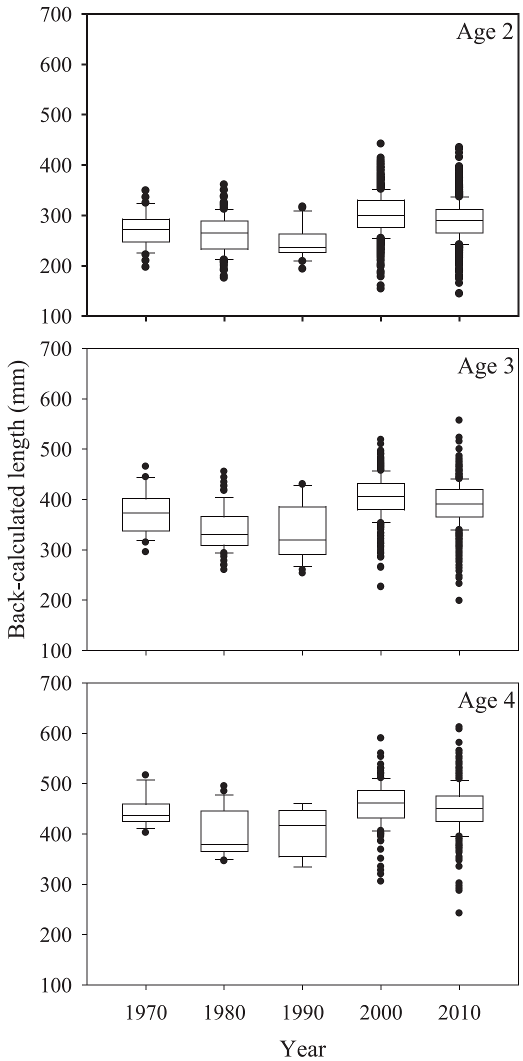

Figure 6. Back-calculated lengths for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho, across five decades. We calculated back-calculated lengths from scales (1970–1990) and otoliths (2000–2020).

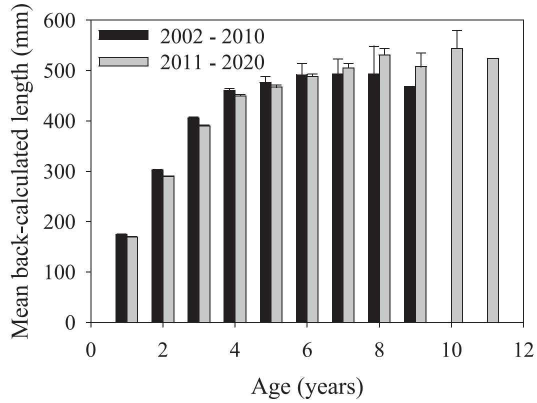

Figure 7. Mean back-calculated lengths and standard error for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho (2002–2020). We calculated mean back-calculated lengths from otoliths.

salmonids. Some climate models predict trout habitat declines of 53% to 97% with warming temperatures (e.g., Flebbe et al. 2006). We included environmental variables that may be related to climate change (e.g., air temperature, snowpack, and reservoir volume) as covariates in our analysis. Interestingly, the only relationship that we detected with these environmental variables was a positive relationship between air temperature and YCT growth. This observation was somewhat surprising given that we hypothesized that growth would slow as temperatures increased. One reason for this observation is that temperatures in Henrys Lake might not be warm enough to have a negative effect on YCT. Minimum air temperature during the growing season (i.e., 1 May to 31 October) has increased since the 1990s, but maximum air temperature has remained relatively constant. Alternatively, Henrys Lake may have enough thermal refuge that YCT are not yet affected by increasing temperatures. Similar patterns have been observed in other systems. Bonneville Cutthroat Trout were able to tolerate normally lethal water temperatures when cycled with cool-water periods (Johnstone and Rahel 2003; Schrank et al. 2003). As such, Bonneville Cutthroat Trout were able to "reset" when cold-water refugia were available. Yellowstone Cutthroat Trout survive in geothermally heated streams (≤27°C) in Yellowstone National Park by using thermal refugia (Varely and Gresswell 1988; Gresswell 2011). Yellowstone Cutthroat Trout in Henrys Lake congregate on springs and near tributaries during peak summer temperatures (McCarrick 2021). Temperatures may rise above thermal tolerances for YCT, but there may be enough thermal refugia to mitigate any negative effects. Although temperature does not appear

Table 2. Top multiple regression models for catch per unit of effort (CPUE) for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho (2002–2020). Explanatory variables include CPUE for Brook Trout *Salvelinus fontinalis* (BKT) and Rainbow Trout *Oncorhynchus mykiss* × Yellowstone Cutthroat Trout hybrids (HYB) in Henrys Lake. We ranked models by Akaike's information criterion for overdispersed data and corrected for small sample sizes ($QAIC_c$). Delta $QAIC_c$, number of parameters (*K*), weight of the model (w_i), and coefficient of determination (McFadden's pseudo R^2) are reported. The direction of the relationship between catch rates and the covariates is indicated (positive [+] and negative [–]).

Model parameters	$QAIC_c$	$\Delta QAIC_c$	K	w_i	R^2
+ BKT CPUE	21.1	0.00	2	0.24	0.18
+ BKT CPUE + HYB CPUE	21.8	0.75	3	0.16	0.25
Null	22.4	1.36	1	0.12	
+ HYB CPUE	22.6	1.53	2	0.11	0.10

Table 3. Top multiple regression models for growth of Yellowstone Cutthroat Trout (YCT) *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho (1994–2019). Explanatory variables include number of YCT stocked annually, minimum air temperature (temperature; °C) during the growing season (1 May–31 October), and catch per unit of effort (CPUE) for Brook Trout *Salvelinus fontinalis* (BKT), Utah Chub (UTC) *Gila atraria*, and all trout in Henrys Lake. We ranked models by Akaike's information criterion for overdispersed data and corrected for small sample sizes (QAIC$_c$). Delta QAIC$_c$, number of parameters (*K*), weight of the model (w_i), and coefficient of determination (McFadden's pseudo R^2) are reported. The direction of the relationship between catch rates the covariates is indicated (positive [+] and negative [–]).

Model parameters	AIC$_c$	ΔAIC$_c$	*K*	w_i	R^2
– BKT CPUE – UTC CPUE + YCT stocking	131.5	0.00	5	0.19	0.56
– UTC CPUE + trout CPUE	131.7	0.17	4	0.17	0.45
– BKT CPUE	131.7	0.20	3	0.17	0.33
– BKT CPUE – UTC CPUE + temperature	131.8	0.26	5	0.16	0.55

to be negatively affecting growth at this time, it might become a concern if temperatures rise.

We observed a negative relationship between YCT growth and Brook Trout catch rates. Most research conducted on interactions between Brook Trout and YCT has focused on streams (Young 1995; Peterson et al. 2004). Results of that research consistently illustrate that Brook Trout are associated with reduced growth and recruitment failure of YCT (Peterson et al. 2004; Gresswell 2011; Al-Chokachy et al. 2018). Limited information is available on the interactions of Brook Trout and YCT in lake systems; however, Donald (1987) documented displacement of Cutthroat Trout and Rainbow Trout by Brook Trout in 88% of lakes in the Canadian mountain national parks with small outlets. Cutthroat Trout and Rainbow Trout became established in only 5% of lakes where Brook Trout, Cutthroat Trout, and Rainbow Trout were stocked together. Although not well understood, Dunham et al. (2002) documented aggressive interactions between Brook Trout and Cutthroat Trout. Brook Trout are more sensitive to temperature than YCT (Cunjak and Green 1986; Young 1995) and may congregate near springs and other cold-water sources during periods of high temperature (i.e., summer), thereby limiting access for the other species like YCT.

The impetus of this project was to understand long-term trends in population dynamics of YCT in Henrys Lake. Although there have been concerns about YCT in Henrys Lake, our research suggests no major changes in the population characteristics. Management goals for Henrys Lake are to maintain 5.4 YCT per net night and that at least 10% of the YCT in annual gillnet surveys be greater than or equal to 508 mm in TL (B.H., unpublished data). Catch rates in Henrys Lake averaged 7.4 YCT per net night from 2002 to 2020. The percentage of YCT greater than or equal to 508 mm in TL has varied from 0% to 20% and averaged 3.4% (±4.5). In 2020, catch rates were 6.4 YCT per net night, with 2% above 508 mm in TL. Creel data further suggest that the YCT population is stable. Angler catch rates have some variation from year to year, but general trends are stable (Heckel et al. 2020). Although Utah Chub abundance was negatively related to YCT growth, YCT are still growing fast. A response from YCT may be observed if Utah Chub abundance continues to increase. Like most systems, continued monitoring using standardized methods will be essential for evaluating YCT and Utah Chub in Henrys Lake. Also, results from this research provide critical information on adfluvial YCT. Adfluvial Cutthroat Trout provide important fisheries, and information on how they function is central to informed management and conservation decisions.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Datafile JFWM-21-074.S1 contains information on the number of fish sampled, sampling effort, total length (mm) of sampled fish, and weight measurements (g) for some years surveyed (i.e., 2004 to 2020) in Henrys Lake, Idaho. We used Henrys Lake raw survey data to calculate catch per unit of effort of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, Rainbow Trout *Oncorhynchus mykiss* × Yellowstone Cutthroat Trout hybrids, Brook Trout *Salvelinus fontinalis,* and Utah Chub *Gila atraria* in Henrys Lake.

Available: https://doi.org/10.3996/JFWM-21-074.S1 (635 KB XLSX)

Data S2. Datafile JFWM-21-074.S2 contains mean back-calculated lengths for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho. Data include year sampled, age at length at capture, growth increments from Image Pro software, structure type, and how we captured the fish for all Yellowstone Cutthroat Trout aged from Henrys Lake, Idaho, 1977 to 2020. We used incremental growth measurements to evaluate changes in growth in the Yellowstone Cutthroat Trout in Henrys Lake, Idaho.

Available: https://doi.org/10.3996/JFWM-21-074.S2 (263 KB XLSX)

Data S3. Datafile JFWM-21-074.S3 Contains stocking records for Henrys Lake, Idaho from 1968 to 2020. We used these data to evaluate factors influencing catch rates (2002 to 2020) and growth (1994 to 2019) of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho. We used the stocking rates of each species as explanatory variables in regression modeling.

Available: https://doi.org/10.3996/JFWM-21-074.S3 (87 KB XLSX)

Data S4. Datafile JFWM-21-074.S4 contains air temperature data for Island Park, Idaho 1989 to 2020. We used these data to evaluate factors influencing catch rates (2002 to 2020) and growth (1994 to 2019) of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho. We calculated a variety of potential covariates from these data and used them as explanatory variables in regression modeling (e.g., average temperature during the growing season).

Available: https://doi.org/10.3996/JFWM-21-074.S4 (413 KB XLSX)

Data S5. Datafile JFWM-21-074.S5 contains Island Park snow course 1938 to 2020 data. We obtained these data from Natural Resources Conservation Service SNOTEL Site 546 in Island Park, Idaho, and used the data to evaluate factors influencing catch rates (2002 to 2020) and growth (1994 to 2019) of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho. We used the stocking rates of each species as explanatory variables in regression modeling.

Available: https://doi.org/10.3996/JFWM-21-074.S5 (31 KB XLSX)

Data S6. Datafile JFWM-21-074.S7 contains Henrys Lake volume data. We used these data to evaluate factors influencing catch rates (2002 to 2020) and growth (1994 to 2019) of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho. We calculated a variety of potential covariates from these data and used them as explanatory variables in regression modeling (e.g., average volume during the growing season).

Available: https://doi.org/10.3996/JFWM-21-074.S6 (386 KB XLSX)

Table S1. Proportion of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* at each age that we sampled from Henrys Lake, Idaho, from 2002 to 2020.

Available: https://doi.org/10.3996/JFWM-21-074.S7 (23 KB DOCX)

Table S2. Parameter estimates and confidence intervals for top regression models. The top multiple regression models for catch per unit of effort (CPUE, number per net night) for Yellowstone Cutthroat Trout (YCT) *Oncorhynchus clarkii bouvieri* in Henrys Lake, Idaho (2002–2020). Explanatory variables include CPUE for Brook Trout (BKT) *Salvelinus fontinalis* and Rainbow Trout *Oncorhynchus mykiss* × YCT hybrids (HYB) in Henrys Lake. Top multiple-regression models for growth of Yellowstone Cutthroat Trout in Henrys Lake, Idaho (1994–2019). Explanatory variables include number of YCT stocked annually, minimum air temperature (temperature; °C) during the growing season (1 May to 31 October), and CPUE BKT, Utah Chub *Gila atraria* (UTC), and all trout in Henrys Lake.

Available: https://doi.org/10.3996/JFWM-21-074.S8 (22 KB DOCX)

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