

ARTICLE

Population Ecology and Evaluation of Suppression Scenarios for Introduced Utah Chub

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Abstract

Introduced Utah Chub *Gila atraria* were first sampled in Henrys Lake, Idaho, in 1993, and their presence in the system is a concern given possible interactions with sport fishes. Our objective was to describe the population dynamics of Utah Chub in Henrys Lake. A total of 362 Utah Chub was sampled via gill nets, with an average catch rate of 20.5 fish/net-night (SE = 6.0) during May 2016. Average TL was 210 mm (SE = 3), and average weight was 134 g (SE = 5). Pectoral fin rays were used to provide estimates of growth and age structure. Utah Chub varied in age from 2 to 12 years, and recruitment was stable (recruitment coefficient of determination = 0.96). Estimated total annual mortality was 40% (SE = 4%). Fecundity of Utah Chub in Henrys Lake increased with length and varied from 6,232 to 156,797 eggs/female. Age-structured population models were constructed using the demographics data, and estimated average population growth rate over a 10-year period was 1.17. This study provides a comprehensive description of Utah Chub population dynamics and insight on their management in systems where they are not native. This information is not only useful for guiding management actions but also serves to further our understanding of Utah Chub ecology.

Introduction of fish outside their native distribution was commonplace throughout the United States in the late 19th and early 20th centuries (Kolar et al. 2010). Originally, the introduction of fish was a popular management tool and the first task of many state fish commissions was to stock fish with the goal of enhancing fishery resources.

Contemporary natural resource agencies have largely stopped the broad-scale introductions given the potentially negative effects of nonnative fishes (Klein et al. 2016). However, fish introductions often occur without agency authorization (Rahel 2004). Regardless of the method of introduction, nonnative fish species have been shown to

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negatively affect native fish assemblages or fisheries (Rinne 1997; Kwak and Freeman 2010). Nonnative fish can negatively affect native fish assemblages through competition (e.g., Taniguchi et al. 2002), predation (e.g., White and Harvey 2001), habitat alteration (e.g., Kolar et al. 2010), and hybridization (e.g., Kanda et al. 2002; Kovach et al. 2011). One example of competition is Ord Creek, Arizona, where introduced Brook Trout *Salvelinus fontinalis* comprised 85% of the total number of fish and 78% of the biomass despite the presence of native Apache Trout *Oncorhynchus apache* (Rinne et al. 1981). Similarly, illegally introduced Burbot *Lota lota* in the Green River basin, Utah and Wyoming, consume native fishes of conservation concern (e.g., Bluehead Sucker *Catostomus discobolus*; Klein et al. 2016).

Fisheries managers may manage introduced or undesirable fish populations through eradication or control efforts (Kolar et al. 2010). Techniques for eradicating or controlling introduced fish populations can be placed into three different categories: chemical (Marking 1992; Lentsch et al. 2001), physical (Johnston 1961; Thompson and Rahel 1996; Ng et al. 2016), and biological (Ward et al. 2008; Schill et al. 2016; Winters et al. 2017). Regardless of the method contemplated, eradication and control efforts in large systems can be expensive (Kolar et al. 2010); thus, knowledge of how much effort is required to influence introduced fish populations is needed prior to the implementation of control programs (Klein et al. 2016; Brauer et al. 2019). Furthermore, it is important to have a comprehensive knowledge of the target species' life history and population dynamics to establish metrics for success and to evaluate various management strategies.

One system where a newly introduced species may be negatively influencing existing fish populations is Henrys Lake, Idaho. Utah Chub *Gila atraria* were first detected and sampled in Henrys Lake in 1993 (Gamblin et al. 2001). Utah Chub in Henrys Lake are of particular interest because their catch rates have increased markedly since 1993 (10 fish/net-night). If Utah Chub densities continue to increase, competition with salmonid sport fish for prey and space may intensify (Sigler and Sigler 1996; Winters and Budy 2015). In Flaming Gorge Reservoir, Utah and Wyoming, introduced Utah Chub had a 99.7% diet overlap with Rainbow Trout *Oncorhynchus mykiss* (Schneider and Hubert 1987). Additionally, Utah Chub in Scofield Reservoir, Utah, have displayed diet overlap with Rainbow Trout and Bonneville Cutthroat Trout *Oncorhynchus clarkii utah* (Winters and Budy 2015). As Utah Chub density increased in Flaming Gorge Reservoir, growth of kokanee *Oncorhynchus nerka* declined dramatically (Teuscher and Luecke 1996). Interactions such as these are cause for concern if Utah Chub are introduced into a system.

Although Utah Chub are widely regarded as having a negative influence on desirable native fish or sport fish populations, surprisingly little is known about their population dynamics, making it difficult for fishery managers to evaluate control or suppression strategies (Winters et al. 2017). Our objective was to describe the population characteristics (i.e., age and growth, mortality, and fecundity) of Utah Chub in Henrys Lake, Idaho. Population demographic data will enhance our knowledge on the ecology of Utah Chub and allow managers to make informed decisions regarding the management of Utah Chub in areas where they have been introduced or where their abundance represents a limitation to other fisheries objectives (Peterson and Evans 2003). Additionally, as so little is known about Utah Chub populations, we used the information on population dynamics to construct an age-based matrix model for evaluating the predicted response of Utah Chub to various management actions designed to reduce abundance.

METHODS

Henrys Lake is a shallow, eutrophic reservoir located 1,857 m above sea level in eastern Idaho (Rohrer and Thorgaard 1986; Figure 1). Prior to the construction of a dam across the outlet in 1923, the lake was nearing extinction (Irving 1955). At full storage, Henrys Lake covers approximately 2,632 ha (Rohrer and Thorgaard 1986). Average depth in Henrys Lake is about 4 m, with a maximum depth of around 6 m. The lake supports a renowned trophy salmonid fishery for Brook Trout, Rainbow Trout

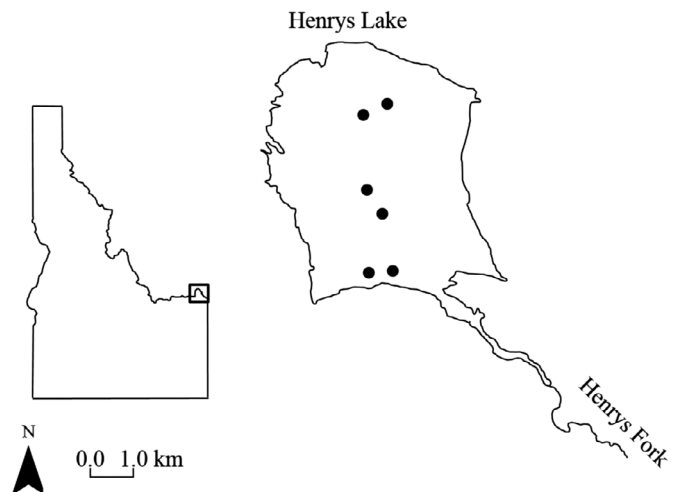


FIGURE 1. Map of Henrys Lake, Idaho, including the outflow (i.e., Henrys Fork). The black circles represent the locations where gill nets were set.

× Yellowstone Cutthroat Trout *O. clarkii bouvieri* hybrids, and Yellowstone Cutthroat Trout (Griffin et al. 2017).

Utah Chub are native to the upper Snake River, Idaho and Wyoming, and the Lake Bonneville basin, Utah (Sigler and Sigler 1996). Utah Chub commonly live 5–8 years but have been documented to live over 12 years (Sigler and Sigler 1996; Griffin et al. 2017; A. Ward, Utah Division of Wildlife Resources, personal communication). Utah Chub are usually <200 mm in length but may exceed 400 mm in some systems. Utah Chub are broadcast spawners and typically spawn in shallow water (i.e., <0.1 m) during late spring and summer (Sigler and Sigler 1996).

Utah Chub were collected from Henrys Lake during May 2016 using experimental gill nets (46 m long × 2 m deep; panels of 2.0-, 2.5-, 3.0-, 4.0-, 5.0-, and 6.0-cm bar-measure mesh). Three sinking gill nets and three floating nets were set at dusk and fished for 12 h. Collected fish were measured for TL (mm) and were weighed (g). The leading left pectoral fin was removed as close to the pectoral girdle as possible for all fish (Koch et al. 2008; Griffin et al. 2017). Fin rays were stored in paper coin envelopes and allowed to air dry. Utah Chub were visually inspected for maturity, and ovaries were removed from the first five mature females per 1.0-cm length-bin. Ovaries were stored in a 15% formalin solution in Whirl-Pak bags (Nasco International, Inc., Fort Atkinson, Wisconsin) prior to analysis.

Dried fin rays were placed in centrifuge tubes and embedded in epoxy following the methods of Koch and Quist (2007). A low-speed saw (Buehler, Inc., Lake Bluff, Illinois) was then used to cut a thin section (~0.3 mm) at the base of the fin ray (Griffin et al. 2017). Fin ray sections were polished, viewed through a dissecting microscope with transmitted light, and evaluated using image analysis software (Image-Pro Plus; Media Cybernetics, Rockville, Maryland). Age was estimated for each fish by enumerating presumed annuli on each structure. Mean back-calculated lengths at age were then estimated for each annulus using the Dahl–Lea method (Lea 1910; Quist et al. 2012; Shoup and Michaletz 2017).

Dynamic rate functions were evaluated using a number of different techniques. Growth was estimated by fitting a von Bertalanffy growth model (von Bertalanffy 1938) to mean back-calculated length-at-age data for each age-class as

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

where L_t is the estimated length of a Utah Chub at time t ; L_∞ is the theoretical maximum average length of fish in the population; K is the growth coefficient; t is the age; and t_0 is the theoretical age when length equals 0 mm

(Quist et al. 2012; Ogle et al. 2017). Instantaneous mortality rate (Z) was calculated using the Chapman–Robson estimator and the “peak plus one” method using age-3 to age-12 fish, as they were assumed to be fully recruited to the gear (Chapman and Robson 1960; Smith et al. 2012). Total annual mortality (A) was calculated as $A = 1 - e^{-Z}$, and all mortality was assumed to be natural mortality (M) as Utah Chub are not targeted by anglers (Ricker 1975). Variability in recruitment was estimated using the recruitment coefficient of determination (RCD; Isermann et al. 2002; Quist 2007).

Fecundity was estimated gravimetrically (Schemske 1974). Ovaries were removed from the formalin solution, rinsed with water, blotted dry, and weighed to the nearest 0.001 g. One ovary from each fish was randomly selected and divided into quarters, and a subsample of eggs was removed from each quarter. Each subsample was weighed to the nearest 0.0001 g, and the number of mature eggs was enumerated under a dissecting microscope (Wydoski and Cooper 1966). Eggs were considered mature when they were at least 0.03 mm and had a yellow-orange color indicating the presence of yolk (Schemske 1974). The number of eggs in each subsample was then divided by the weight of the subsample to calculate eggs per gram for each subsample. Average number of eggs per gram was calculated for the subsampled ovary and multiplied by the total weight of both ovaries to estimate total fecundity.

Population modeling was conducted using a female-based Leslie matrix (Caswell 2000; Klein et al. 2016). Leslie matrices were structured after a prebreeding census as

$$\lambda = \begin{bmatrix} \text{Fert1} & \cdots & \cdots & \text{Fert12} \\ S0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & S12 & 0 \end{bmatrix}$$

where λ represents the population growth rate, Fert1–Fert12 represent fertility rates for Utah Chub from ages 0 to 12, and $S0$ – $S12$ represent age-specific annual survival rate for Utah Chub from ages 0 to 12. Fertility rates for each age t were then calculated following Klein et al. (2016):

$$\text{Fert}_t = f_t \times pm_t \times p_f \times S_0,$$

where f_t is the average fecundity at age t ; pm_t is the probability of maturity at age t ; p_f is the proportion of offspring that are female (0.50); and S_0 is the annual survival rate of age-0 Utah Chub. Annual survival rates for age-0 and age-1 Utah Chub were unavailable and had to be estimated. Age-0 survival was estimated as 0.0012 based on literature values for other cyprinids (i.e., Sharpnose Shiner *Notropis oxyrhynchus*; Wilde and Durham 2007; Peppered

Chub *Macrhybopsis tetranema*: Wilde and Durham 2008). Survival for age-2 to age-12 fish was calculated as $S = e^{-z}$ (Ricker 1975). Annual survival of age-1 fish was assumed to be equal to that of age-2 fish. Probability of maturity at age was estimated by dividing the number of mature female Utah Chub in each age-class by the total number of female Utah Chub in that age-class. The probability of maturity for age-12 female Utah Chub was assumed to be equal to that of age-11 females (i.e., 1.0) because no age-12 female Utah Chub were captured.

The uncertainty associated with fertility and survival rates used to parameterize matrices was accounted for by simulation (Klein et al. 2016; Brauer et al. 2019). Randomly generated vital rates were used to calculate fertility rates for construction of matrices. A beta distribution (i.e., values were constrained between 0 and 1), along with the mean and SE calculated from observed maturity rates, was used to generate the probability of maturity. A log-normal distribution, along with the mean and SE of fecundity from the age–fecundity relationship, was used to generate age-specific fecundity in each simulation. Age-specific survival terms used in each simulation were generated using the mean and SE from estimated survival rates and a beta distribution.

Population growth was evaluated under three management scenarios representing varying levels of exploitation. Instantaneous fishing mortality (F) was allowed to vary from 0.0 to 1.5 in increments of 0.1 within each management scenario (Klein et al. 2016; Ng et al. 2016; Brauer et al. 2019). Management scenarios assumed that fishing mortality was fully selected for age-1 and older, age-2 and older, or age-3 and older Utah Chub. Each management scenario was modeled for a 10-year period. Density dependence was not incorporated into the population modeling due to a lack of information on the relationship between density and various rate functions for Utah Chub (Brauer et al. 2019). No estimate of the total abundance of Utah Chub in Henrys Lake was available. Utah Chub density in Strawberry Reservoir, Utah, is 101.9 fish/ha (Ward, personal communication). Assuming a similar density of Utah Chub in Henrys Lake, 268,307 individuals were used for modeling. Starting values for population simulations were calculated by multiplying the total abundance by the proportion of individuals in each age-class. Age-2 and younger Utah Chub were not fully recruited to the sampling gear, so their abundance was predicted based on the abundance of the other age-classes by using simple linear regression (Caswell 2000; Klein et al. 2016). Management scenarios were then simulated 1,000 times for each level of F using the popbio package (Stubben and Milligan 2007) in statistical package R (R Core Team 2017). Population growth rate (λ_t) was calculated using the formula $\lambda_t = N_t / N_{t-1}$ over ten 1-year time steps, and average λ_t was calculated over all time steps (Klein et al. 2016; Brauer et al.

2019). The average λ_t (λ_g), along with 95% confidence intervals, was then calculated to represent the mean growth rate of the population over the entire 10-year period. The 97.5th and 2.5th percentiles of the 1,000 simulations were used as estimates of confidence intervals (Morris and Doak 2002; Ng et al. 2016). When λ_g was < 1.000 , the population was considered to be declining due to recruitment overfishing (Haddon 2011). The level of F that was required to drop below replacement value was used to calculate the equivalent level of A .

Investigation into which vital rates most influenced λ_g was conducted using an elasticity analysis (i.e., proportional sensitivity; Morris and Doak 2002; Klein et al. 2016; Brauer et al. 2019). The elasticity analysis was conducted by reducing age-specific survival, fecundity, or the probability of maturity by 10% while holding all other vital rates constant. Models were simulated 1,000 times over a 10-year period, and λ_g was calculated following the methods described above. Elasticity (i.e., proportional sensitivity) was then assessed by measuring the percent change in λ_g between the “altered” model and the model with the original vital rates.

RESULTS

A total of 362 Utah Chub was sampled via gill nets, with an average catch rate of 20.5 fish/net-night (SE = 6.0). Utah Chub varied in TL from 112 to 319 mm, with an average TL of 210 mm (SE = 3; Figure 2). Weights varied from 29 to 425 g and averaged 134 g (SE = 5).

Utah Chub varied in age from 2 to 12 years (Figure 3), but the majority (38%) were age 3 or age 4. Mean back-calculated lengths at age varied from 46 mm at age 1–313 mm at age 12 (Table 1). Growth was relatively fast during the first 6 years and then declined. The theoretical maximum average length of the population (L_∞) was estimated to be 361 mm (Figure 4). Total annual mortality (A) was estimated as 40% (SE = 4%). Recruitment was stable for Utah Chub in Henrys Lake (RCD = 0.96). Both male and female Utah Chub first matured at age 2. Approximately 9% of male Utah Chub were mature at age 2, 55% were mature at age 3, and all males were mature by age 5. Twenty-seven percent of female Utah Chub were mature at age 2, 50% were mature at age 3, and all females were mature by age 6. Total fecundity increased with length and varied from 6,232 to 156,797 eggs/female, with an average of 60,549 eggs/female (SE = 4,200; Figure 5).

Population modeling revealed that without fishing mortality (i.e., only natural mortality), the population of Utah Chub in Henrys Lake was predicted to continue to grow (i.e., $\lambda_g = 1.167$, 95% confidence interval = 1.160–1.174; Table 2; Figure 6). By targeting age-1 and older Utah Chub for removal, the predicted population growth rate could be lowered to less than the replacement value once

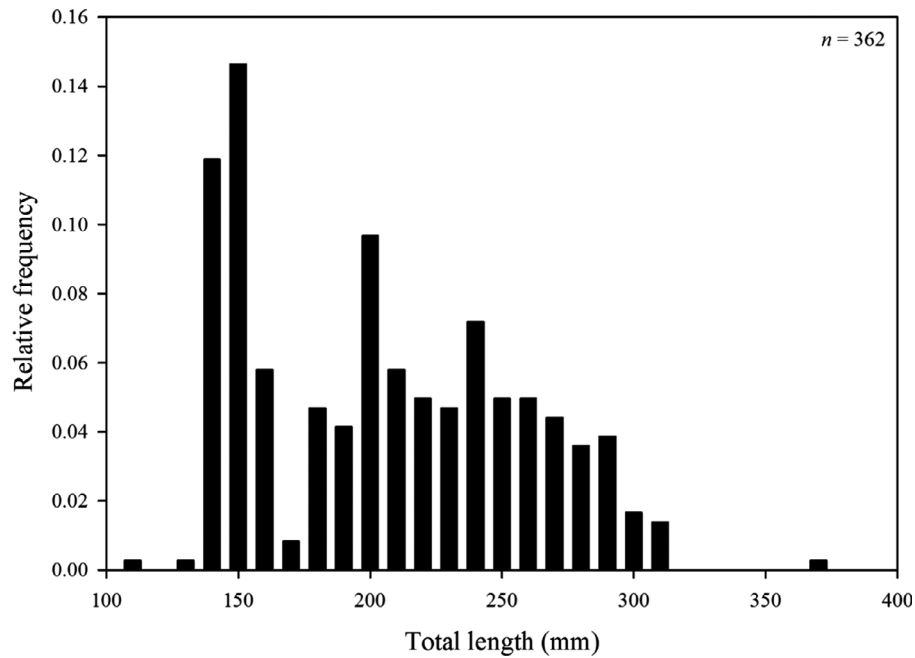


FIGURE 2. Length frequency distribution of Utah Chub sampled via gill nets in Henrys Lake, Idaho (May 2016).

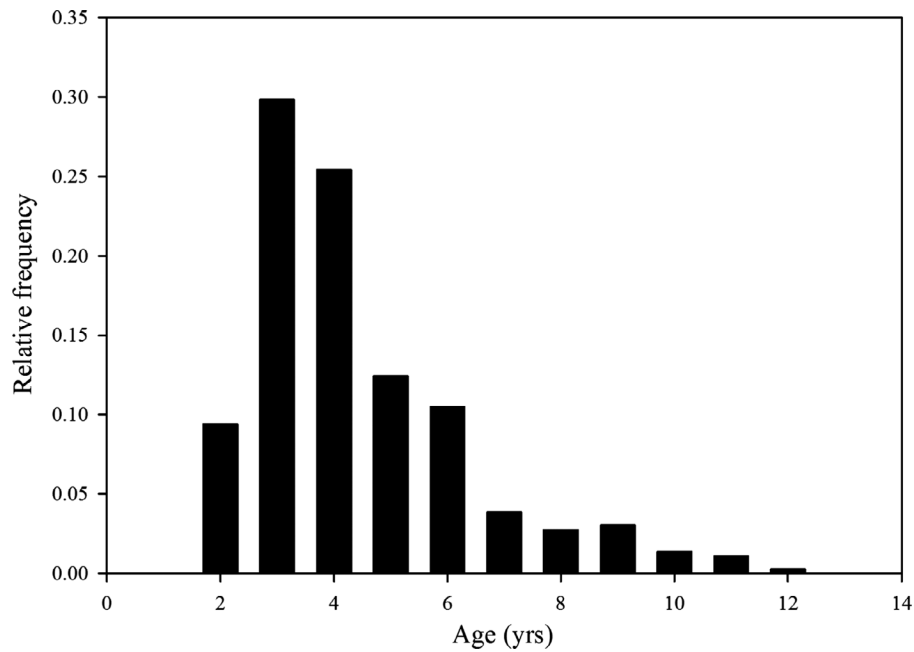


FIGURE 3. Age structure of Utah Chub sampled from Henrys Lake, Idaho, via gill nets (May 2016).

F was equal to 0.20 (i.e., $\lambda_g = 0.990$, 95% confidence interval = 0.980–0.994). If age-2 and older Utah Chub were targeted for removal, a higher level of fishing mortality (i.e., $F = 0.30$) would be needed to cause the predicted population growth rate to drop below replacement level (i.e., $\lambda_g = 0.973$, 95% confidence interval = 0.964–0.981).

Lastly, if age-3 and older Utah Chub were targeted, the predicted population growth rate would be lower than the replacement value once F equaled 0.50, where λ_g was equal to 0.970 (95% confidence interval = 0.959–0.980). Based on these models, A would have to be 51% if age-1 and older fish were targeted for removal, 55% if age-2

TABLE 1. Mean back-calculated length (TL, mm) at age (years) for Utah Chub sampled from Henrys Lake, Idaho (May 2016). Standard errors are shown in parentheses.

Age	Year-class	n	Mean back-calculated length at age:											
			1	2	3	4	5	6	7	8	9	10	11	12
2	2014	34	72.9 (2.8)	149.2 (1.0)										
3	2013	108	52.5 (2.0)	104.0 (2.3)	163.3 (2.1)									
4	2012	92	56.4 (1.9)	118.8 (2.5)	166.9 (2.1)	213.2 (2.1)								
5	2011	45	46.6 (2.6)	103.9 (3.3)	160.4 (2.9)	203.0 (3.2)	240.9 (3.7)							
6	2010	38	50.8 (2.8)	99.8 (3.4)	151.0 (3.5)	193.5 (3.3)	230.3 (3.3)	265.9 (3.4)						
7	2009	14	44.6 (3.7)	83.1 (5.9)	126.0 (6.5)	170.6 (6.7)	205.8 (7.4)	236.7 (7.7)	267.5 (7.3)					
8	2008	10	44.3 (3.9)	82.3 (4.2)	114.2 (6.6)	156.7 (6.5)	195.5 (6.7)	227.6 (6.6)	252.6 (7.4)	278.4 (6.9)				
9	2007	11	43.1 (3.8)	73.9 (4.3)	102.9 (4.6)	136.0 (5.0)	172.1 (4.7)	207.9 (3.5)	235.4 (3.9)	257.5 (3.5)	284.0 (4.2)			
10	2006	5	45.1 (6.7)	75.6 (8.3)	107.9 (9.8)	144.6 (8.8)	171.9 (7.6)	203.8 (5.0)	233.2 (3.8)	256.8 (2.5)	277.2 (2.7)	300.4 (3.0)		
11	2005	4	35.2 (2.8)	69.4 (4.5)	107.6 (6.6)	152.4 (6.6)	180.1 (3.7)	210.4 (2.9)	230.5 (6.2)	255.9 (4.9)	279.4 (2.6)	294.1 (2.5)	312.8 (4.6)	
12	2004	1	42.5 (0.0)	100.6 (0.0)	159.3 (0.0)	210.7 (0.0)	242.6 (0.0)	255.4 (0.0)	263.2 (0.0)	272.8 (0.0)	282.8 (0.0)	287.9 (0.0)	297.9 (0.0)	313.0 (0.0)
Overall		362	53.4 (1.0)	108.4 (1.5)	155.8 (2.9)	195.9 (6.7)	219.9 (9.5)	242.1 (11.3)	249.1 (12.6)	264.4 (13.7)	281.4 (14.9)	296.6 (15.9)	309.8 (16.8)	313.0 (0.0)

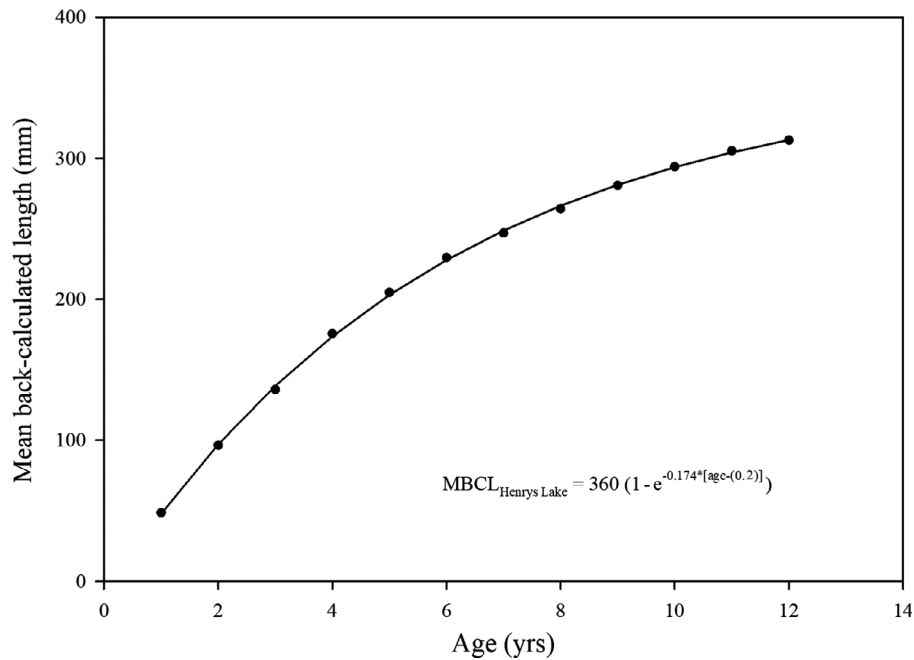


FIGURE 4. von Bertalanffy growth model for Utah Chub ($n=362$) sampled from Henrys Lake, Idaho (May 2016). The dots represent the mean back-calculated length (MBCL) at a given age, and the solid line represents the fitted von Bertalanffy growth model.

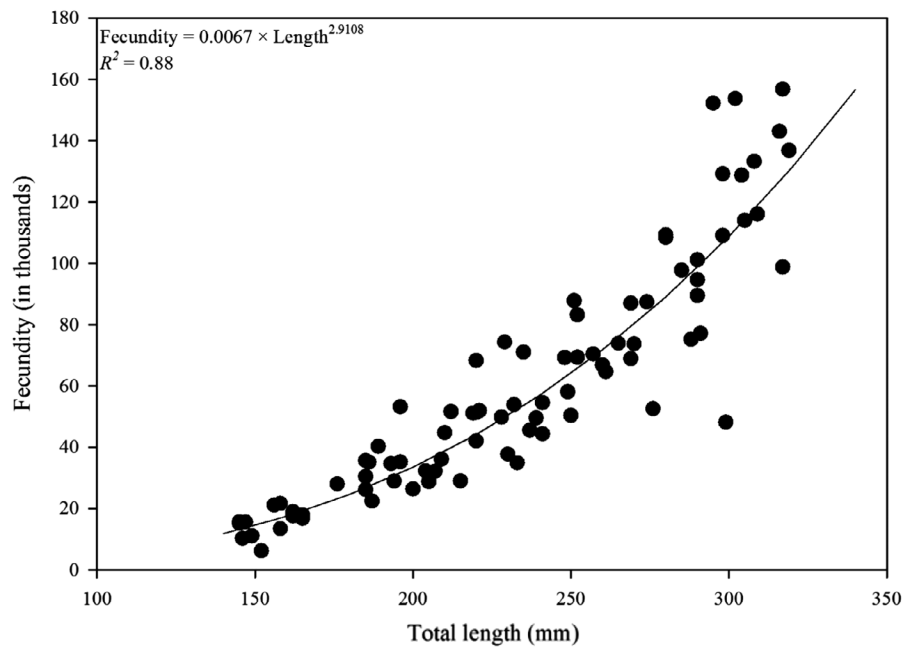


FIGURE 5. Fecundity-length relationship for Utah Chub sampled from Henrys Lake, Idaho (May 2016). The circles represent individual data points, and the solid line represents the fitted regression model.

and older fish were targeted for removal, and 64% if age-3 and older fish were targeted for removal to ensure that the population growth rate is below the replacement value.

Elasticity analysis revealed that λ_g was most sensitive to changes in the survival of age-1 and age-2 Utah Chub and the fecundity of age-2 and age-3 Utah Chub. For example, a 10% reduction in the survival of age-1 and age-2

TABLE 2. Mean vital rates and associated SEs used to construct population matrices for Utah Chub sampled from Henrys Lake, Idaho (May 2016). Results of an elasticity analysis for the population matrices are also included to evaluate which vital rates most influenced the population growth rate (λ_g). Models were simulated 1,000 times over a 10-year period. Population growth rate (λ_t) was calculated using the formula $\lambda_t = N_t/N_{t-1}$ over ten 1-year time steps, and average λ_t was calculated over all time steps. The average λ_t (λ_g) was then calculated to represent the mean growth rate of the population over the entire 10-year period. The elasticity analysis was conducted by reducing age-specific survival, fecundity, or the probability of maturity by 10% while holding all other vital rates constant. Elasticity was then assessed by measuring the percent change in λ_g between the “altered” model and the model with the original vital rates. Vital rates with the largest percent change were considered to have the most influence on λ_g .

Vital rate	Age	Estimate	SE	Percent change in λ_g
Survival (<i>S</i>)	0	0.0012	0.00024	0.02
	1	0.5967	0.02107	2.22
	2	0.5967	0.02107	2.02
	3	0.5967	0.02107	1.72
	4	0.5967	0.02107	1.11
	5	0.5967	0.02107	0.67
	6	0.5967	0.02107	0.42
	7	0.5967	0.02107	0.22
	8	0.5967	0.02107	0.14
	9	0.5967	0.02107	0.08
	10	0.5967	0.02107	0.04
	11	0.5967	0.02107	0.01
	12	0.5967	0.02107	0.01
Fecundity (<i>f</i> ; total eggs/ female)	0	0	0	
	1	0	0	
	2	11,386	2,036	2.19
	3	24,649	2,622	2.00
	4	46,457	3,669	1.74
	5	61,730	4,864	1.10
	6	73,595	7,397	0.69
	7	109,297	11,451	0.43
	8	94,621	5,834	0.22
	9	129,072	17,916	0.14
	10	121,368	7,344	0.08
	11	145,541	5,907	0.03
	12	165,988	6,644	0.01
Probability of maturity for females (<i>pm</i>)	0	0.00	0.00	
	1	0.00	0.00	
	2	0.27	0.09	0.15
	3	0.50	0.06	0.28
	4	1.00	0.00	0.58
	5	1.00	0.00	0.42
	6	1.00	0.00	0.26
	7	1.00	0.00	0.20
	8	1.00	0.00	0.10
	9	1.00	0.00	0.09
	10	1.00	0.00	0.03
	11	1.00	0.00	0.04
	12	1.00	0.00	0.02
Proportion of offspring that are female (<i>p_f</i>)	2–12	0.50		

Utah Chub caused a 2% decline in λ_g (Table 2). Similarly, a 10% reduction in the fecundity of age-2 and age-3 Utah Chub caused a 2% decline in λ_g .

DISCUSSION

Direct comparisons of population dynamics between Utah Chub populations are difficult, as population

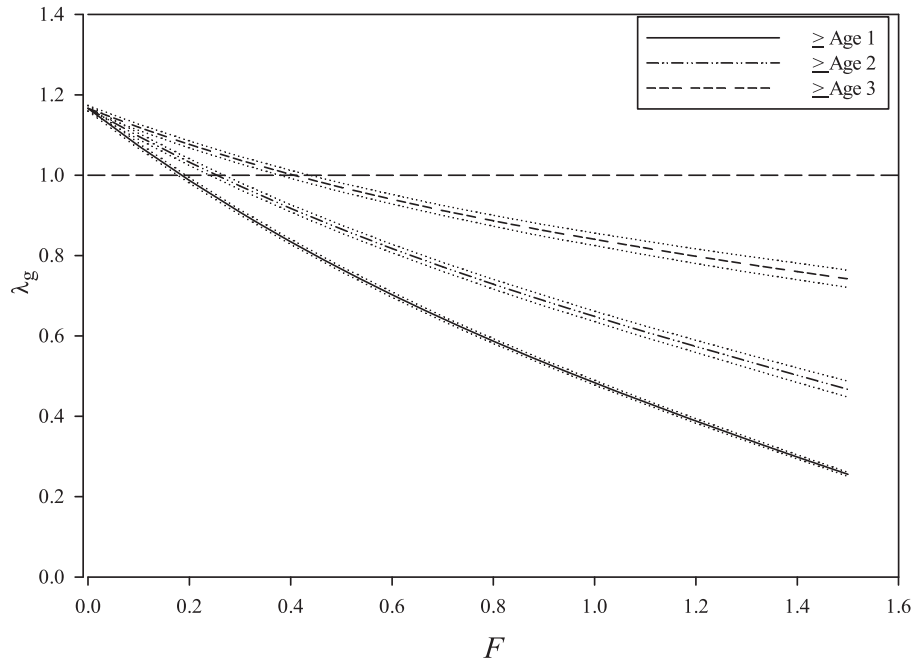


FIGURE 6. Estimated population growth rates for Utah Chub in Henrys Lake, Idaho, projected over 10 years. The dashed horizontal line represents the replacement value (i.e., $\lambda_g = 1.000$). The curved lines represent the population growth rates for age-1 and older, age-2 and older, and age-3 and older Utah Chub in which they were fully selected for in terms of fishing mortality (F). The dotted lines represent 95% confidence intervals.

demographics data are limited. Despite the scarcity of data, information is available for a handful of populations across the distribution of Utah Chub (Neuhold 1957; Graham 1961). In general, Utah Chub sampled in Henrys Lake grew to a large length (>200 mm), were long lived, and displayed relatively slow growth. Utah Chub in Henrys Lake also had very stable recruitment, experienced average mortality rates, and were highly fecund.

Information on age and growth, mortality, and fecundity is not readily available for many Utah Chub populations. Utah Chub in Hebgen Lake, Montana (i.e., 361 mm; Graham 1961); Jackson Lake, Wyoming (i.e., 429 mm; J.M.F., unpublished data); and Strawberry Reservoir, Utah (i.e., 423 mm) achieved greater lengths than Utah Chub in Henrys Lake (i.e., 319 mm). The only other population of Utah Chub from which growth data are available is the Hebgen Lake population (Graham 1961). Growth of Utah Chub in Hebgen Lake was similar to that in Henrys Lake for age-1, age-2, and age-3 fish (Graham 1961). Age-4 and older fish in Hebgen Lake appear to grow slightly faster (12 mm at age 4) than Utah Chub in Henrys Lake. Theoretical maximum average length was lower for Henrys Lake ($L_\infty = 360$ mm) than for Hebgen Lake ($L_\infty = 562$ mm). Despite the longer life span of Utah Chub in Henrys Lake, total annual mortality was similar between the two lakes, with estimates of A equal to 40% in Henrys Lake and 31% in Hebgen Lake (Graham 1961). Total annual mortality of Utah Chub in Henrys Lake was

similar to that in Panguitch Lake, Utah ($A = 40\%$), and lower than that in Navajo Lake, Utah ($A = 61\%$; Neuhold 1957). Because the current study is the first to provide age at maturity and fecundity estimates for Utah Chub, comparisons with other populations were not possible.

Based on the results of our population modeling, the Utah Chub population in Henrys Lake may continue to grow (i.e., $\lambda_g > 1.000$) unless M or F increases. Estimates of A required to cause recruitment overfishing for Utah Chub in Henrys Lake ($A \geq 51\%$) were similar to levels of A reported to cause recruitment overfishing in other populations of introduced fishes. Age-structured population models for Lake Trout *Salvelinus namaycush* in Priest Lake, Idaho, indicated that A would have to be maintained at a level of 52% over 5 years to cause recruitment overfishing (Ng et al. 2016). A similar level of A (58%) was necessary to cause recruitment overfishing for Lake Trout in Lake Pend Oreille, Idaho (Hansen et al. 2008). Additionally, A would have to be over 57% for mature lentic Burbot in the Green River, Wyoming, to cause recruitment overfishing (Brauer et al. 2019). The level of effort required to increase A to a level that would cause Utah Chub in Henrys Lake to experience recruitment overfishing would likely be costly and require a long-term commitment of resources (Quist and Hubert 2004; Kolar et al. 2010).

Given the paucity of information regarding population demographics data of Utah Chub, a number of

assumptions was incorporated into population models. For example, it is worth noting that the models in the current study assumed that survival was the same for age-1 and age-2 fish. If age-1 survival and age-2 survival are not equal, then the estimate of A required to cause recruitment overfishing is an overestimate. The sensitivity analysis indicated that λ_g was most sensitive to age-1 and age-2 survival. Although the overall effect of age-1 and age-2 survival on population growth was $<2\%$, future studies would benefit from better estimates of age-1 and age-2 survival. Another consideration is that the population model developed in our study does not include estimates of density dependence. Suppression of a population can result in compensatory responses in vital rates due to reduced density-dependent interactions (Rose et al. 2001; Weber et al. 2016). Compensatory responses of increased survival (Weber et al. 2016), growth (Brodeur et al. 2001; Weber et al. 2016), and fecundity (Brodeur et al. 2001) have been documented in suppressed fish populations. For instance, Common Carp *Cyprinus carpio* that were subject to suppression in South Dakota lakes displayed a decrease in survival that was slower than expected given the level of exploitation in those systems (Weber et al. 2016). White Sucker *Catostomus commersonii* from five lakes in Quebec, Canada, also displayed a compensatory response in vital rates after suppression (Brodeur et al. 2001). Specifically, the White Sucker population exhibited increased recruitment, increased growth rates, larger size at maturity for females, decreased age at maturity for males, and increased fecundity after suppression. The lack of density dependence in our population models likely results in an underestimate of the fishing mortality required to cause recruitment overfishing as compensation in vital rates would likely occur. As with any management action, monitoring the response of population dynamics to changes in population density is critical and would allow managers to refine models by including informed estimates of density dependence.

Despite the cost, the success of efforts to suppress or completely eradicate unwanted fish populations is not unprecedented. For example, the Lake Trout population in Lake Pend Oreille has been successfully suppressed using an aggressive strategy that includes a bounty system, commercial gillnetting, and trapnetting, but this program costs US\$400,000 annually (Martinez et al. 2009). Complete eradication of Tui Chub *Siphateles bicolor* has also been reported in Diamond Lake, Oregon, through the use of lake drawdowns, commercial gillnetting, and rotenone (Eilers et al. 2011). Although cost estimates are not available for the removal of Utah Chub in Henrys Lake, it has been reported that removal efforts focusing largely on cyprinids can vary from \$2 to \$86 per fish (Mueller 2011). If manual methods prove to be cost prohibitive for controlling or eradicating Utah Chub, then the use of

predatory species, such as Bonneville Cutthroat Trout and tiger trout (Brown Trout *Salmo trutta* × Brook Trout), could offer a less expensive method of control (Ward et al. 2008; Winters and Budy 2015) while providing a sport fishery for anglers. Suppression efforts take many years to accomplish and represent a long-term commitment by agencies. For instance, Hansen et al. (2019) described that if the gillnetting effort was optimized in Lake Pend Oreille, it would take 7–13 years to reduce the Lake Trout population to 90% of its peak abundance and then the effort must be continued indefinitely at a maintenance level. Similarly, it took 3 years of intensive effort to eradicate Tui Chub from Diamond Lake (Eilers et al. 2011).

Results of this study provide a foundational understanding of Utah Chub population dynamics in Henrys Lake. Additionally, this study was the first to produce population simulation models based on demographics data for Utah Chub. The models produced in this study can potentially be used as a reference point for other systems where introduced Utah Chub have become established throughout the western United States, such as Flaming Gorge Reservoir (Schneidervin and Hubert 1987; Teuscher and Luecke 1996), Scofield Reservoir (Winters and Budy 2015), and Hebgen Lake (Graham 1961). Due to the paucity of data describing the population demographics of Utah Chub, making comparisons between the population in Henrys Lake and other populations was difficult. Therefore, further research describing population demographics of Utah Chub in other systems is warranted. Studies reporting age at maturity and fecundity of Utah Chub would be particularly useful. Furthermore, studies incorporating density dependence into population growth models and evaluating gears (e.g., gill nets, trap nets, and trawls) to determine which are the most efficient are also needed. Lastly, studies investigating the occurrence of Utah Chub in trout diets are warranted, as they would provide further insight into the interactions between Utah Chub and other species. Further research would provide managers with greater insight into the general population dynamics and the potential for suppression in systems where Utah Chub are undesirable or overabundant.

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