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ARTICLE

Population Characteristics and Management of Lentic Populations of Nonnative Burbot in the Green River System, Wyoming

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Abstract

Fishes introduced outside of their native distributions have the potential to negatively affect their recipient ecosystems. Since their illegal introduction into the Green River, Wyoming, in the 1990s, Burbot *Lota lota* have been sampled in lotic and lentic environments throughout the Green River system, where they pose a threat to native fishes and valuable sport fisheries. In response to this invasion, managers of the Green River have begun to explore the efficacy of a suppression effort targeting Burbot. We sought to the describe population dynamics of Burbot in the lentic portions (i.e., reservoirs) of the Green River system in comparison with Burbot population dynamics in lotic areas of the Green River. We also sought to evaluate potential management scenarios for a suppression program. Burbot for this study were collected from Fontenelle and Flaming Gorge reservoirs in October and November 2016. Growth rates of Burbot in the lentic portion of the system were higher than those for fish in the Green River. Total annual mortality rates (*A*) of Burbot were approximately 10% lower in the reservoirs (33%) than in the Green River. Additionally, lentic Burbot matured earlier than lotic Burbot. An age-structured population model indicated that Burbot populations were growing rapidly (population growth rate $\lambda = 1.18$) in the study reservoirs. Annual exploitation (μ) of juvenile Burbot would need to reach 7%; the μ of mature Burbot would need to increase to 33% or greater ($A \geq 57\%$) to effectively suppress Burbot in this system. Sensitivity analysis suggested that mortality of age-1 and age-2 Burbot had the greatest influence on λ. However, due to difficulties in collecting juvenile Burbot in the Green River system, focusing removal efforts on mature individuals may be the most realistic option for suppressing Burbot populations in this system.

The introduction of fishes outside of their native distribution continues to be a serious issue for natural resource management agencies. When introduced outside of their native distribution, nonnative species often affect native fish populations through competitive interactions, predation, or habitat alteration or by acting as disease vectors

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(White and Harvey 2001; Taniguchi et al. 2002; Chornesky and Randall 2003; Miller and Crowl 2006; Poulin et al. 2011). For example, nonnative Common Carp *Cyprinus carpio* remove aquatic vegetation and reduce water clarity, thereby reducing primary production and limiting visibility for sight-feeding fishes (Parameswaran et al. 1972; Zambrano et al. 2006; Fischer et al. 2013). Common Carp populations in high abundance have proven to alter aquatic food webs (Parkos et al. 2003). Alterations caused by nonnative fishes are often detrimental to native fish, sport fish, and the overall biodiversity of systems (Jackson et al. 2010).

Although prevention of invasive species is preferred (Leung et al. 2002; Chornesky and Randall 2003), many invasive species become established before management agencies are aware of their presence (Pinder et al. 2005; Britton and Davies 2007). Once an invasive species becomes established, suppression and eradication become the best possible options to mitigate the invader's potential negative effects on native fauna (Kolar et al. 2010). Suppression programs are expensive and difficult, requiring more expense and effort than are often feasible (Chornesky and Randall 2003; Quist and Hubert 2004; Mueller 2005). The high cost and effort required for removal of invasive fishes have been demonstrated in the San Juan River of southeastern Utah. Since the San Juan River Basin Recovery Implementation Program took effect in 1992, average costs associated with the removal of invasive species have grown to nearly US$500,000 annually (USFWS 2016). When resource agencies are faced with such costs, any suppression effort must be supported by an extensive understanding of the invasive species' life history and ecology (Chornesky and Randall 2003; Simberloff 2003; Mueller 2005). For instance, Lake Trout *Salvelinus namaycush* are slow growing and mature at old ages, making them susceptible to overexploitation. Invasive populations of Lake Trout, such as those in Yellowstone Lake, Wyoming, and Lake Pend Oreille, Idaho, have been subject to removal efforts based on population models using demographic data that describe appropriate removal levels (Hansen et al. 2008; Syslo et al. 2011). Regardless of the species targeted for suppression, data on population structure and dynamics are needed before a suppression program can be initiated. The current situation involving invasive Burbot *Lota lota* in the Green River of Wyoming is one such example.

The Burbot is the only freshwater representative of the cod family (Gadidae). Burbot have a circumpolar distribution that rarely extends below 40°N latitude, and they occupy both lotic and lentic environments throughout their distribution (McPhail and Paragamian 2000). The Burbot is a top predator and preys on a variety of fishes and invertebrates (e.g., crayfishes) throughout its life cycle (Hewson 1955; Paragamian 2009; Gardunio et al. 2011; McBaine et al. 2018). In addition, Burbot are highly fecund and exhibit aggregate spawning behavior (McPhail and Paragamian 2000). The majority of Burbot populations throughout the species' distribution are stable; however, populations along the northern tier of the United States are experiencing decline (Stapanian et al. 2010). The decline is especially apparent for populations like those in the Kootenai River, Idaho, and throughout Wyoming (Krueger and Hubert 1997; Hubert et al. 2008; Ireland and Perry 2008). Management of declining populations is primarily focused on the conservation and enhancement of native populations (Paragamian 2000; Dillen et al. 2008; Ireland and Perry 2008; Stapanian et al. 2010; Neufeld et al. 2011). In contrast, management focuses on control and suppression of invasive populations in systems where Burbot are invasive. Such contrary management objectives are present in Wyoming.

Burbot are native to the Wind–Bighorn and Tongue River systems of Wyoming (Baxter and Stone 1995). Burbot have been extirpated from the Tongue River and are currently experiencing population decline in the Wind–Bighorn River system (Krueger and Hubert 1997; Hubert et al. 2008; Underwood et al. 2016). Their imperiled status in these systems has motivated their classification as a "species of greatest conservation need" throughout their native distribution in Wyoming (WGFD 2017). Conversely, Burbot were illegally introduced into the Green River basin during the 1990s (Gardunio et al. 2011). Since their introduction, they have become established and are regularly sampled in lotic and lentic portions of the Green River (Gardunio et al. 2011; Klein et al. 2016; Smith et al. 2016). Nonnative Burbot pose a threat to ecologically important native fishes (i.e., Bluehead Sucker *Catostomus discobolus*, Flannelmouth Sucker *Catostomus latipinnis*, Roundtail Chub *Gila robusta*, and Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus*) as well as economically important sport fishes (e.g., Brown Trout *Salmo trutta*, Rainbow Trout *O. mykiss*, Smallmouth Bass *Micropterus dolomieu*, and kokanee *O. nerka*) through direct predation and competitive interactions (Klobucar et al. 2016; McBaine et al. 2018). Due to the possible deleterious effects of Burbot, the Wyoming Game and Fish Department (WGFD) has begun to explore the efficacy of a Burbot suppression program in the Green River basin. Such a program will depend on the collection of demographic data on Burbot populations throughout the Green River system.

Demographic data serve as the basis for fisheries management and can provide insight on recruitment dynamics, trophic interactions, and resource availability (Guy and Brown 2007; Allen and Hightower 2010; Quist et al. 2012). Estimates of population dynamic rates (i.e., growth, recruitment, and mortality) are critical for developing population models as well as for monitoring a population's response to suppression efforts (Cambray 2003). For example, Klein et al. (2016) developed a population model that predicted the response of the nonnative Burbot population to various levels of exploitation in the Green River, Wyoming. This was achieved by collecting and analyzing demographic data from Burbot in the upper and lower portions of the Green River. Simulations indicated that high exploitation rates would be necessary to successfully suppress the Burbot population in riverine habitats. As beneficial as this research has been to managers, a significant knowledge gap remains regarding the efficacy of a suppression program in the system. Burbot occupy both lotic and lentic habitats in the Green River basin (i.e., Fontenelle Reservoir, Flaming Gorge Reservoir, and the Green River), but the population characteristics of Burbot in the reservoirs have not been described previously. Additionally, data from Burbot in reservoirs were unavailable and therefore were not included in previous modeling efforts. Given that dynamic rates likely differ between lotic and lentic populations of Burbot (e.g., mortality and growth rates; Fisher et al. 1996), any differences that exist between lotic and lentic Burbot populations may affect the application of the previously developed model. To assess the applicability of previous modeling efforts, demographic estimates for Burbot occupying lentic habitats in the Green River system are needed for comparison with estimates from Burbot in lotic habitats. Assessment of differences in the population characteristics between lotic and lentic Burbot and subsequent differences in management (e.g., exploitation goals) will provide a better understanding of the requirements of a future suppression program.

The objective of our study was to describe the population characteristics of Burbot in Fontenelle and Flaming Gorge reservoirs. We then estimated the appropriate exploitation goals that would be needed to suppress the Burbot population below replacement level in lentic portions of the Green River. In addition, we compared the population characteristics of lentic Burbot with those of lotic Burbot populations in the Green River and populations from the species' native distribution. Results of this study will further guide Burbot management in the Green River basin and provide insight into the population ecology of Burbot outside of their native distribution.

METHODS

The Green River originates in the Wind River Range of Wyoming and flows approximately 235 km southward before entering Fontenelle Reservoir. Fontenelle Reservoir is an artificial impoundment that is primarily used for flood control, with a secondary use of hydroelectric power generation (Figure 1). At capacity, the reservoir has a surface area of approximately 3,200 ha and a maximum depth of 30 m. From Fontenelle Reservoir, the Green River continues to flow another 125 km before entering Flaming Gorge Reservoir, which straddles the Wyoming–Utah border. Flaming Gorge Reservoir is primarily located in Sweetwater County, Wyoming, whereas the southernmost portion of the reservoir is located in Daggett County, Utah. Flaming Gorge Reservoir is primarily used for hydroelectric power generation. At capacity, the reservoir has a surface area of 17,000 ha and a maximum depth of 133 m.

Native species present in the system include the Bluehead Sucker, Colorado River Cutthroat Trout, Flannelmouth Sucker, Mountain Whitefish *Prosopium williamsoni*, Roundtail Chub, Mottled Sculpin *Cottus bairdii*, and Speckled Dace *Rhinichthys osculus*. Common nonnative fishes include the Brown Trout, kokanee, Lake Trout, Smallmouth Bass, Rainbow Trout, White Sucker *Catostomus commersonii*, and Burbot (WGFD 2017).

Burbot were collected from Fontenelle and Flaming Gorge reservoirs in October and November 2016 by using trammel nets. All nets were deployed in randomly assigned standardized sampling locations used by the WGFD. Trammel nets measured 48.8 m long and 1.8 m deep. Nets consisted of 25.4-cm bar outer mesh and 2.5-cm bar inner mesh. Nets were placed perpendicular to shore at varying depths and fished for approximately 12 h. In an effort to increase sample size, Burbot were also collected from one fishing tournament on Fontenelle Reservoir in January 2017 and two tournaments on Flaming Gorge Reservoir in February 2016 and 2017. Estimates of dynamic rates (i.e., mortality and growth) using tournament data were found to be concordant with those calculated using fishery-independent data (Brauer et al. 2018).

Captured Burbot were enumerated and measured for TL (mm) and weight (g). Sex and maturity status were determined by visual examination of gonads (Hewson 1955). Mature males possessed angular, engorged gonads, whereas immature male gonads were similar in shape but much smaller in size. Mature females had engorged, rounded ovaries that were highly vascularized. Immature females possessed ovaries that were similar in shape but were much smaller and lacked vascularization. Sagittal otoliths were removed from up to 10 Burbot per 10-mm length-group and were stored in 2-mL centrifuge tubes prior to age analysis. Ovaries were removed from up to five mature females per 50-mm length-group and were stored in 5% formalin solution prior to fecundity estimation. Ovaries were only collected from fish that were captured using trammel nets.

Sagittal otoliths were mounted in epoxy and transversely sectioned about the nucleus (Koch and Quist 2007; Klein et al. 2014). Cross sections were examined with a dissecting microscope using transmitted light. Annuli were

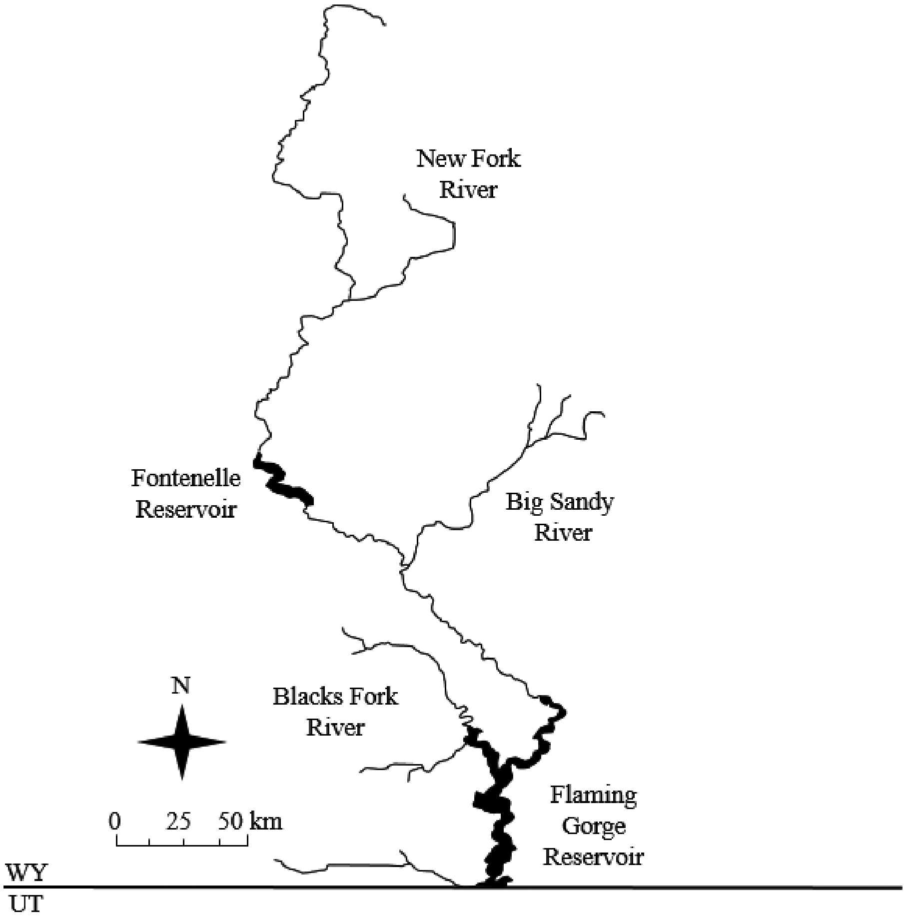

FIGURE 1. Map of the Green River basin, including its major tributaries and associated reservoirs. Burbot were sampled from Fontenelle and Flaming Gorge reservoirs, Wyoming, during autumn and winter (2016–2017).

enumerated by one reader that possessed previous experience in aging hard structures. The reader assigned ages to each otolith without prior knowledge of fish length or sampling location.

Both ovaries from mature female Burbot were blotted dry and weighed to the nearest 0.001 g. One ovary was then randomly selected for fecundity analysis. Subsamples were removed from the posterior, medial, and anterior sections of each selected ovary. These subsamples were weighed to the nearest 0.001 g, and eggs were enumerated (Murua et al. 2003). The number of mature eggs in each subsample was then divided by the weight of that subsample to estimate the number of eggs per gram. The number of eggs per gram for each subsample was averaged and multiplied by total ovary weight to estimate the total number of eggs per ovary. Mean fecundity at age was calculated for age-2 and older female Burbot. Fecundities of missing age-classes were estimated by fitting a linear regression model to the age–fecundity data and predicting fecundity for the missing age-classes (Klein et al. 2016).

Analysis was conducted using the Fisheries Stock Assessment package in R (Ogle 2016). Length structure was summarized using the proportional size distribution (PSD; Gabelhouse 1984; Fisher et al. 1996; Nuemann et al. 2012). Growth was evaluated with a von Bertalanffy growth model (Quist et al. 2012; Ogle et al. 2017). A nonlinear function was fitted to back-calculated length-at-age data from subsampled Burbot by using the following equation:

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

where L_t is length at time t; L_∞ is the theoretical mean maximum length of Burbot in the population; K is the growth coefficient; t is age; and t_0 is the theoretical age when length equals 0 mm (Quist et al. 2012; Ogle et al. 2017). Mean back-calculated length at age was calculated for Burbot by using the Dahl–Lea method (Campana 1990; Shoup and Michaletz 2017).

The instantaneous rate of mortality (Z) for age-3 and older Burbot was estimated using the Chapman–Robson estimator and the "peak plus one" criterion (Chapman and Robson 1960; Smith et al. 2012). No estimate of Z was available for age-0 Burbot in this system, so an estimate from the literature was used (Paragamian et al. 2011; Klein et al. 2016). Estimates of Z for age-1 and age-2 Burbot were also unavailable, so an average of Z-values for age-0 and age-3 fish was used as an estimate of age-2 mortality. An average of Z for age-0 and age-2 Burbot was used as an estimate for age-1 mortality (Table 1). Similar methods were used by Klein et al. (2016). The instantaneous natural mortality rate (M) was calculated using the Hoenig (1983) equation. Estimates of M and Z were converted to an annual survival rate (S) by using the relationship $S = e^{-M} = e^{-Z}$ (Ricker 1975; Miranda and Bettoli 2007). This survival rate (i.e., based on M) was used to estimate the current level of exploitation in the system and was also used as the estimate of survival for age-3 to age-12 Burbot in our population model. Survival of age-1 and age-2 Burbot was estimated using the averages described above.

TABLE 1. Mean vital rates and SEs estimated for Burbot sampled from Fontenelle and Flaming Gorge reservoirs, Wyoming, during autumn and winter (2016–2017). Vital rate estimates were used to construct population matrices and to model population growth.

Symbol	Description	Age (years)	Estimate	SE
f_t	Total fecundity	2	23,510	46,384
		3	183,799	36,612
		4	344,088	28,544
		5	504,377	23,968
		6	664,666	24,890
		7	824,955	30,821
		8	985,244	39,570
		9	1,145,534	49,668
		10	1,305,823	60,444
		11	1,466,112	71,592
		12	1,626,400	104,627
m_t	Probability of maturity (females)	2	0.330	0.086
		3	0.790	0.049
		4	0.820	0.032
		5	0.960	0.027
		6	1.000	
		7	1.000	
		8	1.000	
		9	1.000	
		10	1.000	
		11	1.000	
		12	1.000	
p_f	Proportion female	2–12	0.500	
S_0	Survival at age	0	0.002	0.0004
S_1		1	0.177	0.039
S_2		2	0.353	0.079
S_{3-12}		3–12	0.705	0.0092

A female-based Leslie matrix was employed to estimate population growth rates of Burbot in the Green River reservoirs (Caswell 2000; Morris and Doak 2002). Demographic rates were virtually identical between the study reservoirs; therefore, data from both reservoirs were pooled to construct a single population model. Matrices were constructed as

$$A = \begin{bmatrix} Fert_1 & \dots & \dots & Fert_{12} \\ S_1 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & S_{11} & 0 \end{bmatrix},$$

where $Fert_1$ through $Fert_{12}$ are fertility rates for age-0 through age-12 Burbot; and S_1 through S_{11} are the corresponding rates of age-specific annual survival at age t. Fertility rates for each age t were calculated as

$$Fert_t = (f_t)(m_t)(p_f)(S_0),$$

where f_t is the mean fecundity at age t; m_t is the probability of maturity for females 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 Burbot (Table 1).

Population growth simulations accounted for uncertainty in the vital rates used to parameterize matrices. Fertility rates included in matrices were calculated from randomly generated vital rates in each simulation. The probability of maturity was generated from a beta distribution (i.e., values constrained between 0 and 1) using the mean and SE calculated from the observed maturity rates. Age-specific fecundity in each simulation was generated from a lognormal distribution using the mean and SE of fecundity from the age–fecundity relationship. Estimated survival rates and their SEs were incorporated into simulations by generating age-specific survival terms using a beta distribution (Caswell 2000; Morris and Doak 2002).

Three hypothetical management scenarios were created to model Burbot population growth (λ). Under these scenarios, instantaneous fishing mortality (F) was allowed to vary from 0 to 1.5 in increments of 0.1, and F fully selected for either age-1 and older Burbot, age-2 and older Burbot, or age-3 and older Burbot. Management scenarios were chosen to account for uncertainty in sampling efficiency for various Burbot age-classes. Our model did not incorporate density dependence due to a lack of information regarding density-dependent relationships for Burbot. A starting population of 20,000 female individuals was used for modeling since no estimate of population size (N) was available. Our models did not include density-dependent functions given the lack of information on how the density of Burbot is related to various rate functions. Abundance starting values for each age-class were obtained by multiplying total abundance by the proportion of each age-class in our sample. Scenarios were run through 1,000 iterations for each level of F by using the R package "popbio" (Stubben and Milligan 2007; R Development Core Team 2014). Population growth rate (λ_t) was calculated each year over ten 1-year-long time steps as $\lambda_t = N_t/N_{t-1}$, and the mean λ_t was calculated over all time steps. The geometric mean of λ_t (λ_G) along with its 95% confidence interval was then calculated to represent the average population growth rate over 10 years. The Burbot population was assumed to be experiencing recruitment overfishing when λ_G dropped below replacement ($\lambda_G < 1$; Haddon 2001). The level of F at which λ_G dropped below 1 was used to calculate the equivalent rate of exploitation.

A sensitivity analysis was conducted to evaluate age-classes that were most sensitive to age-specific mortality. A conventional simulation approach was used to calculate sensitivities (Cross and Beissinger 2001). Age-specific survival was reduced by 10%, and population growth was simulated 1,000 times while holding all other vital rates constant. Sensitivity of age-specific survival was calculated as the percent reduction in λ_G between altered and unaltered matrices over a 10-year period that was averaged over 1,000 replicates. We assumed no fishing mortality when calculating sensitivities.

RESULTS

In total, 923 Burbot were collected from Fontenelle (n = 506) and Flaming Gorge (n = 417) reservoirs. Burbot were large and varied in TL from 218 to 985 mm, with a mean of 534 mm (Figure 2). Proportional size distribution for Burbot was 90 in Fontenelle Reservoir and 79 in Flaming Gorge Reservoir. Incremental PSD values were all higher in Fontenelle Reservoir.

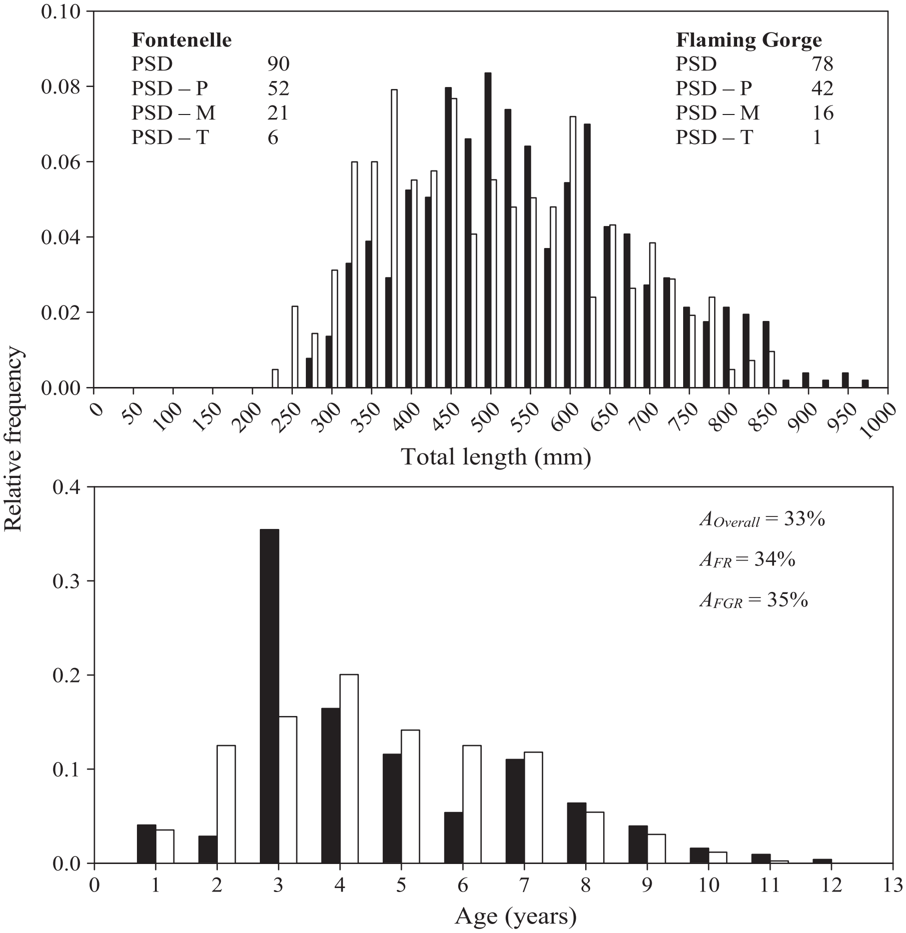

FIGURE 2. Length and age distributions of Burbot sampled in Fontenelle Reservoir (FR; black bars) and Flaming Gorge Reservoir (FGR; white bars), Wyoming, during autumn and winter (2016–2017). Proportional size distributions are provided for stock (PSD), preferred (PSD-P), memorable (PSD-M), and trophy (PSD-T) size classifications. Total annual mortality ($A_{Overall}$, A_{FR}, and A_{FGR}) estimates are also provided.

Ages of Burbot in our sample varied from 1 to 12 years (Figure 2). Total annual mortality (*A*) of Burbot in reservoirs was approximately 33%, and estimated *M* was 29%. Given these estimates, angler exploitation was approximately 4%. The von Bertalanffy growth model indicated that Burbot grew rapidly and could attain large sizes in the study reservoirs (Figure 3). Female Burbot attained larger lengths than male Burbot, but differences in sex-specific growth were minimal.

Female Burbot first began to mature at age 2, which corresponded to a mean length of 300 mm. In our sample, 33% of age-2 female Burbot were mature. All female Burbot were mature at age 6, which corresponded to a mean TL of 596 mm (Table 1). Fecundity for female Burbot increased with age (Figure 4). Mean fecundity was 183,799 eggs (SE = 36,612) for age-3 Burbot and 1,305,823 eggs (SE = 60,444) for age-10 Burbot (Table 1).

Over a 10-year period, λ_G for lentic Burbot in the Green River system was 1.23 assuming no fishing mortality and 1.18 with the current estimate of exploitation (Figure 5). In the scenario where fishing mortality focused on age-1 and older Burbot, λ_G dropped below replacement when *F* was 0.15 or greater. This corresponded to an annual exploitation rate (μ) of 7%. If fishing mortality selected for age-2 and older Burbot, λ_G would drop below replacement when *F* was 0.25 or greater ($\mu \geq 14\%$). In the final scenario, where age-3 and older Burbot were fully selected, the population would experience recruitment overfishing when *F* was at least 0.49 ($\mu \geq 33\%$). Population growth rate λ_G was most sensitive to mortality of age-1 and age-2 Burbot (Figure 6). However, reductions in population growth when selecting for these ages were still minimal. For example, a 10% reduction in survival of age-1 Burbot resulted in a 4% reduction in λ_G over 10 years, and a 10% reduction in survival of age-2 Burbot only resulted in a 3% reduction in λ_G over 10 years.

DISCUSSION

The Burbot is a top predator and has the potential to negatively influence important native and sport fish assemblages in the Green River system (Rudstam et al. 1995; Fratt et al. 1997; Gardunio et al. 2011; Hares et al. 2015; McBaine et al. 2018). Klobucar et al. (2016) evaluated the trophic interactions of Burbot in Flaming Gorge Reservoir and found that Burbot had a relatively high level of diet overlap with Rainbow Trout (18–22%) and Smallmouth Bass (44%). In addition to potential competitive interactions, those authors suggested that Burbot could consume nearly double the biomass of Rainbow Trout annually stocked into Flaming Gorge Reservoir (>1 million individuals). Similarly, McBaine et al. (2018) found that fish composed an average of 75% of the Burbot's diet in the Green River. Given the potential of Burbot to negatively influence the Green River system, a suppression program may be warranted. Determining the efficacy of such a program depends on an in-depth understanding of Burbot

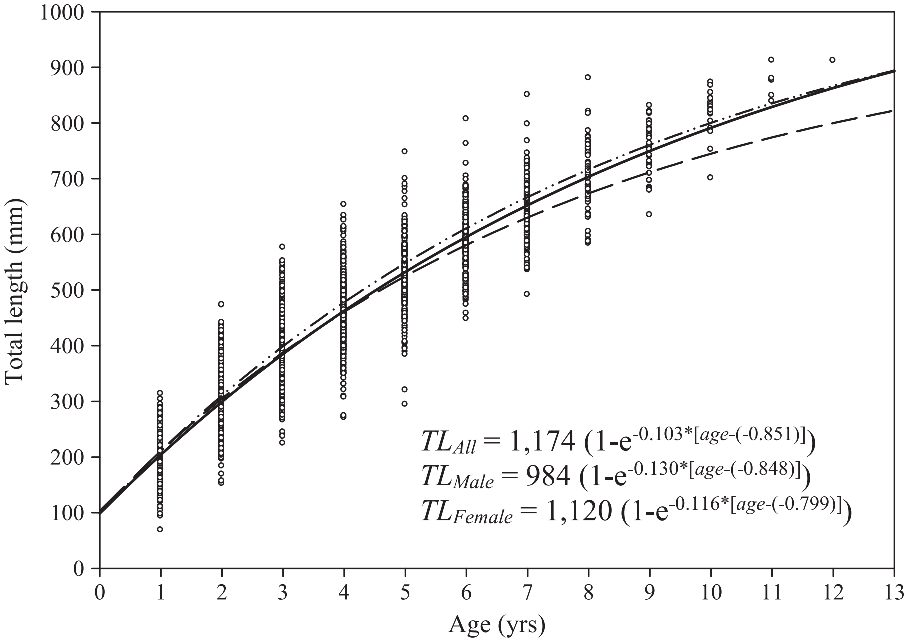

FIGURE 3. Back-calculated TL at age and von Bertalanffy growth models for female Burbot (dotted–dashed line), male Burbot (dashed line), and both sexes combined (solid line). Fish were sampled in Fontenelle and Flaming Gorge reservoirs, Wyoming, during autumn and winter (2016–2017).

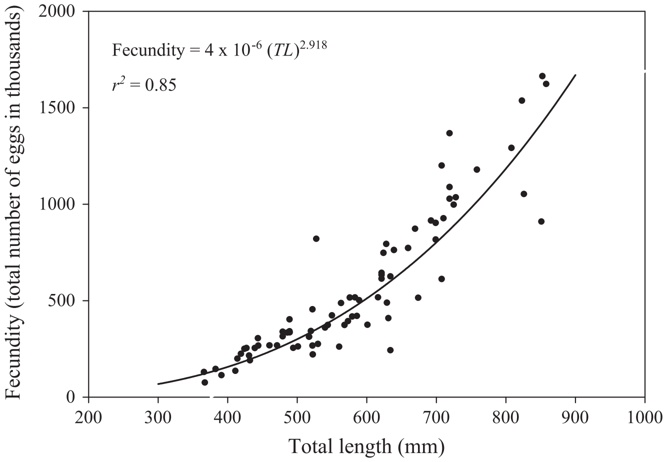

FIGURE 4. Fecundity–TL relationship for female Burbot sampled in Fontenelle and Flaming Gorge reservoirs, Wyoming, during autumn (2016). The solid line and equation represent the fitted regression model. The r^2 value is provided as an estimate of model fit.

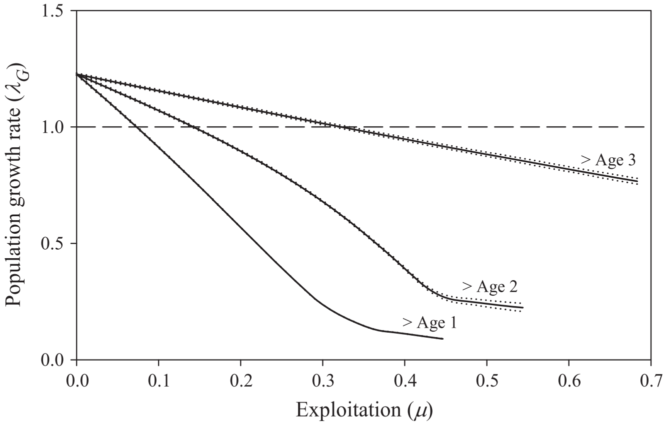

FIGURE 5. Geometric mean population growth rate (λ_G) over a 10-year time period for Burbot sampled from Fontenelle and Flaming Gorge reservoirs, Wyoming, during autumn and winter (2016–2017). Population growth was calculated by assuming that fishing pressure fully selected for age-1 and older Burbot, age-2 and older Burbot, and age-3 and older Burbot. Dotted lines represent 95% confidence intervals for λ_G estimates. The horizontal dashed line represents $\lambda_G = 1$ (i.e., replacement).

population dynamics. This study revealed marked differences in demographic rates between lentic and lotic portions of the Green River Burbot population. Burbot sampled in major reservoirs experienced low mortality rates, grew rapidly, and attained large sizes. Additionally, they matured at an early age and were highly fecund. In contrast, Burbot in lotic portions of the system had higher mortality rates, lower growth potential, and a slower maturity schedule than those in our study (Klein et al. 2016). Given the observed demographic differences, it appears that the lentic portion of the Burbot population in the Green River basin is growing in abundance at a faster rate than the lotic portion.

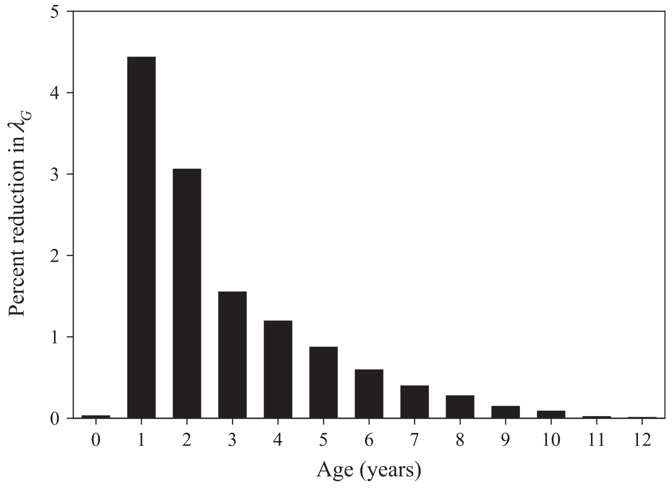

FIGURE 6. Percent reduction in the geometric mean population growth rate (λ_G) given 10% reductions in age-specific survival of Burbot in Fontenelle and Flaming Gorge reservoirs, Wyoming, which were sampled during autumn and winter (2016–2017).

Estimates of Burbot mortality in our study reservoirs were low in comparison with Burbot sampled from the Green River and with Burbot populations in the species' native distribution. Burbot in our study had an *A*-value of 33%, with a small proportion attributed to fishing mortality. Klein et al. (2016) found that Burbot in the lotic portions of the Green River had higher mortality rates ($A = 43\%$). Due to low levels of exploitation in lotic environments of the Green River, the estimate of *A* was also assumed to be the natural mortality level. Estimates of *A* in the lentic portions of the Green River were also lower than those reported for other lentic populations throughout the species' distribution. For example, *A*-values varying from 43% to 63% have been reported for Burbot across various Wisconsin lakes, and values from 54% to 64% have been estimated for Burbot in lakes and reservoirs of the Wind River basin, Wyoming (Schram 2000; Hubert et al. 2008; Lewandowski et al. 2017). The low estimates of mortality from our study are likely due to the relative lack of fishing effort present in this system. Although no empirical estimate of angler exploitation exists for Burbot in the Green River, our estimate of μ is low (4%) compared to those reported for other river systems in Wyoming (Krueger and Hubert 1997). Data from reward tags collected at angling tournaments held on the study reservoirs suggest that our Burbot exploitation estimate may be slightly low for Flaming Gorge Reservoir but not for Fontenelle Reservoir (WGFD, unpublished data). Despite the lack of a robust empirical estimate, exploitation likely does not currently exceed 10% in either reservoir. Tagging studies to elucidate the current exploitation of Burbot in these reservoirs may be warranted.

Burbot in reservoirs of the Green River displayed higher growth rates than Burbot in the lotic portions of the system. Specifically, age-3 and age-6 Burbot in the Green River had mean TLs of 319 and 521 mm, whereas Burbot of the same ages in the Green River reservoirs were 434 and 601 mm. Growth of Burbot in lentic portions of the Green River was comparable to that observed in other Burbot populations experiencing low exploitation. In Upper Red Rock Lake, Montana, age-3 Burbot had a mean length of 501 mm, and age-6 Burbot had a mean length of 682 mm (Katzman and Zale 2000). Von Bertalanffy models fit to our data also suggested that reservoir-dwelling Burbot had a higher value of L_∞ (1,174 mm) than Burbot in the Green River (L_∞ = 779 mm; Klein et al. 2016).

Maturity of Burbot is largely a function of length (Evenson 1990; Bernard et al. 1993; Hubert et al. 2008). The rapid growth rate of Burbot in our study resulted in an accelerated maturity schedule relative to their lotic counterparts. Klein et al. (2016) found that Burbot in the Green River first matured at age 3 and reached 100% maturity at age 8. In comparison, Burbot in our study first matured at age 2, and all Burbot were mature at age 6. Ages at maturity in our study were comparable to those in other lentic Burbot populations. In Lake Winnipeg, Canada, female Burbot began to mature at age 3 and reached 100% maturity at age 7 (Hewson 1955). In Lake Superior, Burbot started to mature at age 2, and all age-5 Burbot were mature (Bailey 1972).

Given their comparably fast growth and large size structure, reservoir populations of Burbot in the Green River system had relatively high reproductive potential. Throughout their distribution, Burbot fecundity rates are generally high, often exceeding 1 million eggs/individual (Lawler 1963; Bailey 1972; Roach and Evenson 1993). Bailey (1972) found that the average fecundity of Burbot in Lake Superior was 812,300 eggs/female. Similarly, Lawler (1963) found that fecundities varied from 74,800 to 1,362,000 eggs/female and averaged 500,000 eggs/female in Heming Lake, Manitoba. Fecundity of Burbot in our study reservoirs was comparable to that of Burbot in the Green River and throughout the species' distribution. Fecundities of Burbot in the Green River varied from 53,000 eggs (250 mm) to 2,099,000 eggs (682 mm), with an average of 621,000 eggs/individual (Klein et al. 2016). We found that the fecundities of lentic Burbot varied from 71,000 eggs (368 mm) to 1,666,000 eggs (852 mm) and averaged 560,000 eggs/individual.

An age-structured population model indicated that the population growth of Burbot in the study reservoirs was faster than that for lotic populations. Early maturity, fast growth, and low mortality of lentic Burbot suggested that these reservoir populations will continue to grow without some form of intervention. Our model indicated that Burbot populations in the study reservoirs would increase at a rate of 23% annually in the absence of exploitation and 18% annually given the current estimate of exploitation. Previous research in the system suggests that the lotic population of Burbot will grow at a rate of 11% annually under similar conditions (Klein et al. 2016). One limitation of our study was the reliance of our models on assumptions of juvenile survival and spawning frequency. Our model used an empirical estimate of juvenile Burbot survival based on a study in which Burbot were reared in earthen ponds and subjected to predation (Paragamian et al. 2011). However, a lack of refuge habitat available to Burbot in that study may have left juveniles overly exposed to predation. Despite this shortcoming, the estimate from Paragamian et al. (2011) was also used by Klein et al. (2016) to model age-0 Burbot survival and is believed to be the best available representation of juvenile Burbot mortality in the Green River system. If juvenile survival in the Green River is higher than the estimate used in our model, then our estimate of population growth rate is an underestimate. We also assumed that Burbot in Green River reservoirs spawned annually. Burbot have been observed to skip spawning, with spawning frequencies of 60–95% (Evenson 1990; Pulliainen and Korhonen 1993). In Burbot populations with low juvenile survival, spawning frequency has been identified as a major driver of population viability (McPhail and Paragamian 2000; Worthington et al. 2011). This suggests that any deviation from the "worst-case scenario" of 100% spawning frequency would likely result in a slower population growth rate for Burbot in the study reservoirs. Furthermore, our models did not consider the movement dynamics of Burbot. Preliminary results of a separate study evaluating movement suggest that a portion of the Green River Burbot population exhibits an adfluvial life history (T. A. Brauer, M. C. Quist, D. T. Rhea, and T. W. Laughlin, unpublished data). Movement of Burbot between lotic and lentic habitats may affect the estimates of our model since a portion of the reservoir population of Burbot is not reproducing in a reservoir. If Burbot from the study reservoirs are spawning in the Green River, then our model results may represent an overestimate of population growth. Additionally, model estimates from Klein et al. (2016) may be underestimates if the spawning activity of adfluvial fish was not accounted for in the modeling of population growth.

Relatively low angling effort could suppress Burbot in our study reservoirs if young age-classes are effectively removed. Unfortunately, trammel nets and anglers were only effective at capturing age-3 and older Burbot (Brauer et al. 2018). Trammel nets have been shown to be the most effective means of sampling Burbot in lentic environments throughout Wyoming during the spring and fall seasons (WGFD, unpublished data). However, trammel nets require extended handling time and may not be the most cost-effective method. Recreational anglers can also act as an effective removal mechanism. Excessive angler exploitation has been implicated in the declining population status of native Burbot populations elsewhere in Wyoming (Hubert et al. 2008). Additionally, Burbot tournaments held on the reservoirs of the Green River have resulted in the removal of approximately 40,000 Burbot from the system since 2010 (Brauer et al. 2018). Unfortunately, angling for Burbot in Wyoming is almost exclusively conducted during the winter, when reservoirs are covered with ice. Other gears, such as gill nets, have been used to capture Burbot. Hewson (1955) reported that Burbot catch rates in gill nets were high enough that commercial harvesters considered them a nuisance. However, gill nets may result in substantial bycatch (Murphy et al. 1995; Buchanan et al. 2002). The shortcomings associated with these methods may make a combination of methods the most appropriate approach for suppression efforts. Additionally, the scenario in which age-3 and older Burbot were selected for removal is likely the most realistic scenario for our study system. Under this scenario, μ would need to exceed 33% annually ($A \geq 57\%$) to effectively suppress Burbot in the study reservoirs. In comparison, Klein et al. (2016) suggested that exploitation of age-3 and older Burbot would need to reach levels of 14% or higher ($A \geq 60\%$) to suppress Burbot in the lotic portions of the system. Given the difference between population demographics and model outputs, using the higher μ estimate (33%) as a suppression target in both lotic and lentic portions of the system may be warranted. Although this level of exploitation will likely require substantial effort (Quist and Hubert 2004; Britton et al. 2011), similar programs have been successful for other invasive species elsewhere in the United States. In Lake Pend Oreille, Idaho, a combination of gillnetting, trapnetting, and angling has resulted in nonnative Lake Trout exploitation rates of over 44%, which exceeded the mortality required to suppress that population (Hansen et al. 2008). Although these efforts have been relatively successful, they come with a large financial burden. For example, the Lake Trout removal program on Lake Pend Oreille has incurred costs of over US$400,000 annually since its initiation (Martinez et al. 2009).

Burbot populations in our study exhibited demographic rates similar to those reported for other lentic populations of Burbot throughout the species' native distribution. However, Burbot in our study grew faster, matured earlier, and had lower mortality than Burbot in the lotic portions of the Green River system. Given the lack of information on nonnative Burbot populations, this study provides crucial insight on their ecology and management outside of their native distribution. Burbot populations in the lotic and lentic portions of the Green River are growing rapidly, and control of Burbot in this system will likely be an arduous process. It is unknown whether the high population growth rates observed in this study are the result of rapid initial population growth exhibited by many invasive species. The short temporal window of our study and lack of similar data from earlier in the invasion process limit our capacity to determine the stage of population growth at which Burbot are operating. Regardless of the stage of establishment, Burbot in the Green River system seem to be prospering in their recipient ecosystem. As is the case with many invasive fish suppression programs, exploitation will need to reach high levels, and this will require considerable effort by management agencies. However, given the proper impetus and application of effort, the suppression of Burbot in this system is likely a tenable goal. By understanding the population characteristics of Burbot in the Green River system and having an idea of the best options for a suppression effort, managers can design and implement an effective suppression program. In the event that Burbot continue to expand outside of their native distribution, this study may also provide beneficial information about how Burbot populations react to new ecosystems and the potential requirements of their management.

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