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ARTICLE

Population Characteristics and the Suppression of Nonnative Burbot

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Abstract

Burbot *Lota lota* were illegally introduced into the Green River, Wyoming, drainage and have since proliferated throughout the system. Burbot in the Green River pose a threat to native species and to socially, economically, and ecologically important recreational fisheries. Therefore, managers of the Green River are interested in implementing a suppression program for Burbot. We collected demographic data on Burbot in the Green River (summer and autumn 2013) and used the information to construct an age-based population model (female-based Leslie matrix) to simulate the population-level response of Burbot to the selective removal of different age-classes. Burbot in the Green River grew faster, matured at relatively young ages, and were highly fecund compared with other Burbot populations within the species' native distribution. The age-structured population model, in conjunction with demographic information, indicated that the Burbot population in the Green River could be expected to increase under current conditions. The model also indicated that the Burbot population in the Green River would decline once total annual mortality reached 58%. The population growth of Burbot in the Green River was most sensitive to age-0 and age-1 mortality. The age-structured population model indicated that an increase in mortality, particularly for younger age-classes, would result in the effective suppression of the Burbot population in the Green River.

In the United States, there is a long history of intentional fish introduction (Rahel 2004). During the latter part of the 19th century, many states developed fish commissions whose primary task was to propagate fish species for recreational and commercial uses. For instance, the territory of Wyoming established a Board of Fish Commission in 1882, the mission of which was to "procure and distribute fish to public waters" with the intent of promoting "the increase and preservation of food fish" (Barkwell 1883). Many states had similar motivations, which led to the unrestrained introduction of fishes throughout the United States. Although the widespread introduction of sport fishes was once common, natural resource management agencies now realize the potential negative consequences of nonnative fish introductions. For example, Lake

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Trout *Salvelinus namaycush* have been shown to negatively affect native salmonid populations in ecosystems where they have been successfully introduced (Fredenberg 2002; Vander Zanden et al. 2003; Martinez et al. 2009). Although it is increasingly uncommon for natural resource management agencies to introduce nonnative fishes, unauthorized introductions continue to occur (Rahel 2004).

One example of an illegally introduced fish species is Burbot *Lota lota* in the Green River drainage of Wyoming. In the 1990s, Burbot were illegally introduced into Big Sandy Reservoir, Wyoming. Following their introduction, Burbot became established in Big Sandy Reservoir and began dispersing downstream into the Green River (Gardunio et al. 2011; Figure 1). Since their initial introduction, Burbot have been sampled from Flaming Gorge Reservoir, Wyoming–Utah, upstream to the confluence of the New Fork and Green rivers (Anna C. Senecal, unpublished information). Burbot are now widely distributed throughout the upper Green River (upstream of Flaming Gorge Reservoir) and represent a major concern for natural resource management agencies in Wyoming.

Burbot is the only freshwater member of the family Gadidae (Howes 1991). It has a circumpolar distribution that rarely extends below 40°N and occupies a diversity of lentic and lotic habitats throughout Eurasia and North America (McPhail and Paragamian 2000). Burbot are highly fecund, with estimates varying from 6,300 (Miller 1970) to 3,477,699 eggs per female (Roach and Evenson 1993). Burbot are generally categorized as piscivores, with some authors estimating that over 80% of the species' diet consists of fish (McPhail and Paragamian 2000). However, recent research suggests that Burbot have fairly plastic diets as adults (Paragamian 2009; Gardunio et al. 2011). Gardunio et al. (2011) estimated that crayfishes *Astacoidea* spp. were present in 75% of the

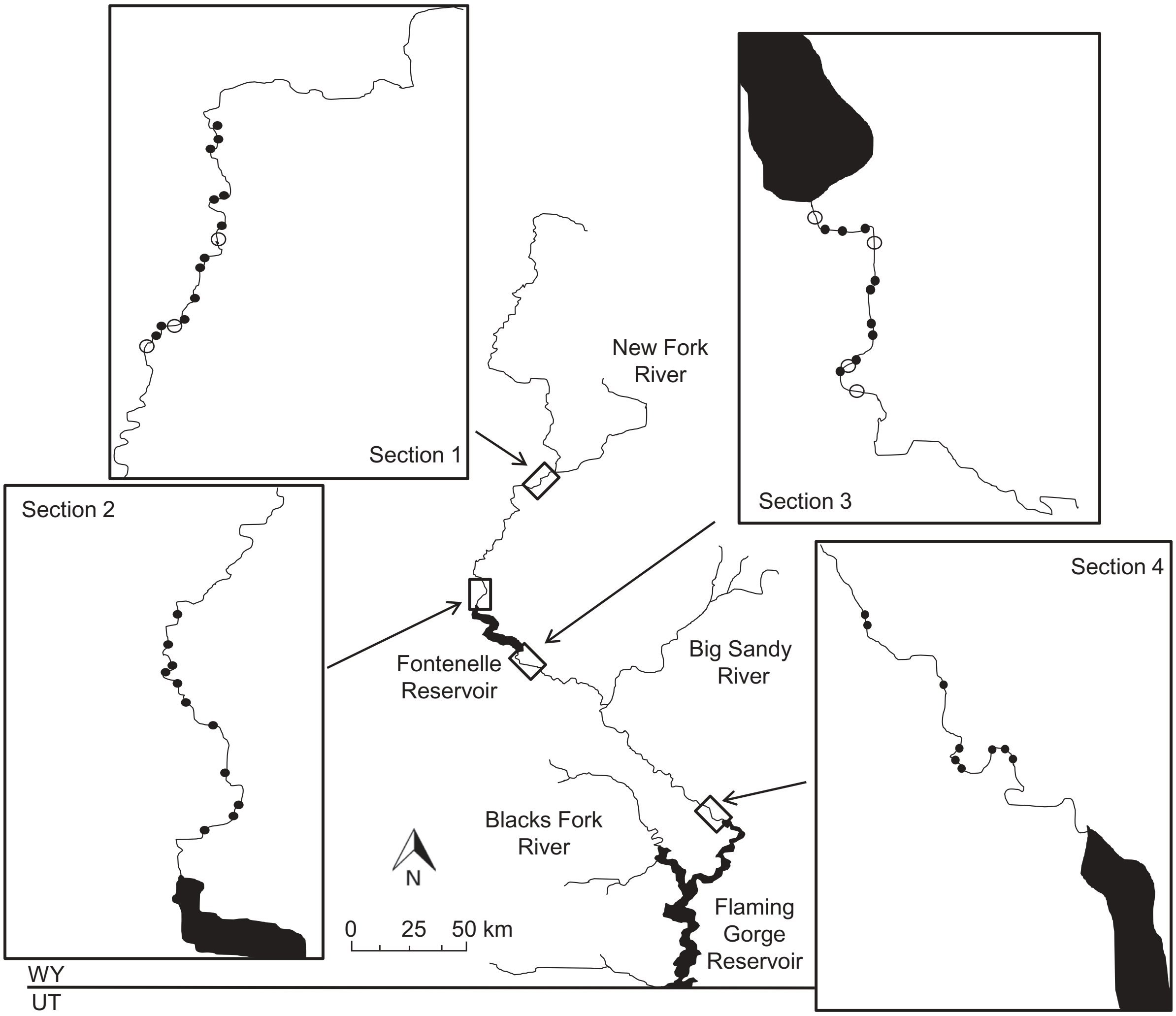

FIGURE 1. River sections used for Burbot sampling in the Green River, Wyoming, during the summer and autumn of 2013. Sites sampled in the summer are denoted by filled circles; additional sites sampled in the autumn are denoted by open circles.

stomachs of the Burbot sampled in Flaming Gorge Reservoir. Regardless of their specific diet, Burbot have the potential to alter the food web of the Green River through direct predation and interspecific competition. The widespread proliferation of Burbot throughout the Green River drainage raises concerns regarding the management of socially and economically important recreational fisheries (e.g., Brown Trout *Salmo trutta*, Smallmouth Bass *Micropterus dolomieu*). In addition, the presence of Burbot in the Green River is troubling with regards to the conservation of native fishes (i.e., Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus*, Bluehead Sucker *Catostomus discobolus*, Flannelmouth Sucker *Catostomus latipinnis*, Roundtail Chub *Gila robusta*). To counteract the potential negative effects of Burbot, the Wyoming Game and Fish Department is interested in controlling the distribution and abundance of Burbot in the Green River drainage.

Established fish populations can be eradicated or controlled through long-term suppression programs (Britton et al. 2011). Although desirable, eradication is often viewed as an impossible objective due to the relatively high expense and difficulty of removing every individual (Britton et al. 2011). Thus, control of unwanted species is often left to long-term suppression programs. Long-term suppression programs attempt to maintain fish populations at an abundance that minimizes their deleterious effects (Simberloff 2003; Mueller 2005). Although a number of physical (e.g., removal, barriers), chemical (e.g., rotenone, antimycin), and biological (e.g., pheromones, genetic manipulation, predation) techniques are available to control unwanted fishes (Tyus and Saunders 2000; Britton and Brazier 2006; Britton et al. 2008), little can be learned about the efficacy of a control program unless demographic data are available. Demographic data provide valuable insight into recruitment dynamics, trophic interactions, and the availability of resources and are the basis for fisheries management (Guy and Brown 2007; Allen and Hightower 2010; Quist et al. 2012). Additionally, understanding population dynamics is critical for evaluating population growth and the response of a population to suppression (Morris and Doak 2002; Cambray 2003). To guide the management of Burbot in the Green River, we undertook research to describe the population characteristics of Burbot and to construct an age-based matrix model to evaluate their response to various management actions.

METHODS

The Green River is the largest tributary of the Colorado River and drains approximately 124,578 km^2 in portions of Wyoming, Utah, and Colorado (Figure 1; Wyoming Game and Fish Department 2010). The Green River originates in the Wind River Range of western Wyoming and flows for approximately 235 km before entering Fontenelle Reservoir. From Fontenelle Reservoir, the Green River flows for 150 km until entering Flaming Gorge Reservoir at the Wyoming–Utah border. From Utah, the river flows through portions of Colorado before returning to Utah, where it joins the Colorado River. Twelve species and subspecies of fish are native to the Green River; however, the Colorado Pikeminnow *Ptychocheilus lucius*, Bonytail *Gila elegans*, and Razorback Sucker *Xyrauchen texanus* have been extirpated from Wyoming (Wyoming Game and Fish Department 2010). The Green River is also home to five species of conservation concern (i.e., Bluehead Sucker, Flannelmouth Sucker, Roundtail Chub, Colorado River Cutthroat Trout, and Mountain Whitefish *Prosopium williamsoni*). In addition to Burbot, 28 nonnative fishes have been introduced into the Green River drainage (Bezzerides and Bestgen 2002; Wyoming Game and Fish Department 2010).

Sampling was conducted in four river sections (two upstream of Fontenelle Dam and two downstream of Fontenelle Dam; Figure 1) during the summer (May 22–July 12, 2013) and two river sections (one upstream of Fontenelle Dam and one downstream) during autumn (September 6–25, 2013). The sections were not the units of interest; rather, they were simply used to allocate sampling effort. Each section was divided into 150-m-long reaches. In total, forty-nine 150-m-long reaches were randomly selected for sampling ($n = 41$ in summer; $n = 28$ in autumn). Reaches were sampled with large-mesh hoop nets (19-mm bar mesh), small-mesh hoop nets (6.4-mm bar mesh), and night electrofishing as part of a larger gear comparison study (Klein et al. 2015). Each reach was sampled with a single gear per day. A sampling event was considered a consecutive 3-d period that consisted of sampling with a small-mesh hoop net, a large-mesh hoop net, and night electrofishing. Sampling events were replicated over a 9-d period, such that each reach was sampled three times with each gear. Due to logistical constraints associated with spring runoff, the summer sampling season commenced at the most downstream section and continued upstream until all reaches were sampled. During the fall, 19 reaches were added to the 41 reaches sampled in the summer to increase sample size. However, because of unusually high precipitation and logistical constraints, only the most upstream reaches ($n = 15$; section 1, Figure 1) and the reaches immediately downstream of Fontenelle Dam ($n = 13$; section 3) were sampled during autumn.

The small-mesh hoop nets had seven 0.6-m-diameter hoops and an overall length of 3 m. In the event of a lost net, a fish "escape route" was placed between the sixth and seventh hoops. The escape routes consisted of 20-cm × 20-cm square openings covered with 6.4-mm bar measure mesh secured with 3-mm untreated cotton twine. In the event of a lost net, the cotton twine would deteriorate, allowing fish to escape. The large-mesh hoop nets had four 0.91-m-diameter hoops and an overall length of 2.9 m. Each net had a "mammalian escape hatch" placed between the third and fourth hoops consisting of a 20-cm × 41-cm opening covered with a 36-cm × 61-cm section sewn on three sides. Each net was positioned parallel to the current with the cod end anchored upstream. Hoop nets were randomly assigned to each reach on the first day of each sampling event. Previously placed hoop nets were removed the following day and replaced with the other size of hoop net. Nets were baited with dead White Sucker *Catostomus commersonii*, a nonnative species in the system, and fished for approximately 12 h. Night electrofishing was conducted on the third day of each sampling event using a drift boat equipped with a 5,000-W generator and a Smith-Root VVP-15B electrofisher (Smith-Root, Inc., Vancouver, Washington). Electrofishing power output was standardized to 2,750–3,200 W (Miranda 2009). One netter was positioned on the bow of the boat with a 2.4-m-long dip net with 6-mm bar knotless mesh. Electrofishing proceeded downstream from the uppermost point of each 150-m reach. Effort was recorded as the total number of seconds that electricity was applied to the water.

All Burbot captured were enumerated, measured for total length to the nearest millimeter, and weighed to the nearest gram. Burbot sampled on the last day of sampling (autumn) were euthanized with an overdose of MS-222 (tricaine methanesulfonate; Western Chemical, Inc., Ferndale, Washington). Euthanized Burbot were visually inspected for maturity, and sagittal otoliths and ovaries were removed. Otoliths were dried, stored in 2.0-mL centrifuge vials, and returned to the University of Idaho for age and growth analysis. Ovaries were preserved in 4% formalin and returned to the University of Idaho for fecundity analysis.

Sagittal otoliths were used to estimate the age and growth of the Burbot. Otoliths were mounted in epoxy in 2.0-mL centrifuge tubes and transversely sectioned about the nucleus (Edwards et al. 2011). Otolith cross sections were approximately 0.5 mm thick. Cross sections were examined using a dissecting microscope with transmitted light and an image analysis system (Image-Pro Plus; Media Cybernetics, Silver Spring, Maryland). Annuli were enumerated independently by two readers without knowledge of fish length and sampling location. Both readers had experience enumerating annuli of various structures prior to the study. After each reader assigned an age, age estimates were compared. If discrepancies existed between age estimates, the structure was re-aged by both readers and discussed in a mutual reading. If a consensus age could not be reached, the structure was removed from further analysis. An age–length key was used to estimate the age and length distributions for all Burbot sampled during the summer and autumn (Isely and Grabowski 2007; Quist et al. 2012).

Sex and maturity were evaluated by visual examination of the gonads of Burbot sampled during autumn (Hewson 1955). Mature males had angular, engorged gonads; the gonads of immature males were similar in shape but greatly reduced in size. Females were considered mature if they possessed round, engorged ovaries that were highly vascularized. Immature females had similarly rounded ovaries, but they were much smaller and lacked apparent vascularization. The sex ratio used for population simulation was estimated from empirical data. Logistic regression was used to predict the age-specific probability of maturity (pm_t) for male and female Burbot because not all age-classes were represented in autumn samples.

The fecundity of up to five sexually mature female Burbot per 5-cm length bin was estimated gravimetrically (n = 45; Murua et al. 2003). Both ovaries of individual fish were blotted dry and weighed to the nearest 0.001 g; then one ovary was randomly selected for fecundity analysis. Subsamples were removed from the posterior, medial, and anterior sections of each ovary and weighed to the nearest 0.001 g and eggs were enumerated (Murua et al. 2003). The number of eggs in each subsample was divided by the weight of the subsample to estimate the average number of eggs per gram. The numbers of eggs per gram from the different subsamples were averaged and multiplied by the total ovary weight to estimate the total number of eggs per ovary (Murua et al. 2003). Fecundity at age (f_i) was estimated by age-class for age-3 and older female Burbot using linear regression. Nonlinear regression was used to estimate the fecundity–length relationship of female Burbot.

The instantaneous total mortality rate (Z) of age-3 to age-9 Burbot was estimated from catch data from the least selective gear (small-mesh hoop nets) using the Chapman–Robson estimator and the peak criterion (Chapman and Robson 1960; Smith et al. 2012). No estimate of Z was available for age-0 Burbot in natural systems; therefore, two estimates of Z were used in an attempt to bracket the instantaneous mortality rate of age-0 Burbot in the Green River (Worthington et al. 2011; Table 1). The "high" estimate of Z was calculated as the mean survival rate of eight groups of hatchery-produced Burbot stocked into earthen ponds for 9 months (Vught et al. 2008). The "low" estimate of Z was obtained from a study in which two groups of Burbot were stocked into earthen ponds and subjected to predation (Paragamian and Laude 2009).

Estimates of mortality for age-1 and age-2 Burbot were not available. Mortality is generally assumed to be highest in the larval stages and to decrease with fish age and size (Houde 1997; Jennings et al. 2001). Therefore, Z was estimated for age-2 Burbot as the average of age-0 and age-3 Burbot mortality, assuming the high and low age-0 mortality rates. Age-1 Burbot mortality was then estimated as the average of age-0 and age-2 Burbot mortality, assuming the high and low age-0 mortality rates. Although estimated values of Z for either age-0 or age-3 and older Burbot could have been applied to age-1 and age-2 Burbot (i.e., a fixed value of Z), these estimates would likely have been unrealistic for age-1 and age-2 Burbot considering the generally assumed decrease in mortality with fish age (Jennings et al. 2001). All estimates of Z were assumed to be equal to the instantaneous natural mortality rate (M) because of limited angler exploitation of Burbot in the Green River (Darren T. Rhea, unpublished data). Instantaneous fishing mortality (F) was incorporated into the population models to evaluate different

TABLE 1. Mean vital rates and SEs estimated from Burbot sampled from the Green River, Wyoming, during the summer and autumn of 2013 that were used to construct population matrices.

Symbol	Description	Age	Estimate	SE
f_t	Fecundity (total eggs/female)	3	217,799	25,033
		4	419,730	87,159
		5	621,660	18,789
		6	823,591	65,089
		7	1,025,521	65,990
		8	1,227,452	86,402
		9	1,429,382	108,720
pm_t	Probability of maturity of females	3	0.536	0.051
		4	0.609	0.101
		5	0.786	0.109
		6	0.919	0.034
		7	0.800	0.103
		8–9	1.000	
p_f	Proportion female	3–9	0.500	
	Survival at age (high)	0	0.041	0.009
S_0				
S_1		1	0.188	0.038
S_2		2	0.335	0.066
$S_{3–8}$		3–8	0.577	0.021
	Survival at age (low)			
S_0		0	0.002	0.0004
S_1		1	0.146	0.006
S_2		2	0.289	0.011
$S_{3–8}$		3–8	0.577	0.021

management scenarios. Instantaneous fishing mortality was allowed to vary from 0 to 1.5 in increments of 0.1. Age-specific estimates of Z were converted to annual survival rates (S) by means of the relationship $S = e^{-z}$, where $Z = F + M$ (Miranda and Bettoli 2007). Age-specific estimates of S were used for population modeling.

A female-based Leslie matrix was used to model the population growth rate of Burbot in the Green River (Caswell 2001; Morris and Doak 2002). Projection matrices were structured after a prebreeding census with the form

$$\mathbf{A} = \begin{bmatrix} \text{Fert}_1 & \dots & \dots & \text{Fert}_9 \\ S_1 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & S_8 & 0 \end{bmatrix},$$

where Fert_1–Fert_9 are fertility rates for age-0 through age-9 Burbot and S_1–S_8 are the age-specific annual survival rates of Burbot at ages 1–8. The fertility rate for each age t were calculated as

$$\text{Fert}_t = f_t \cdot m_t \cdot p_f \cdot S_0,$$

where f_t is the mean fecundity at age t, pm_t is the probability of maturity for females at age t, p_f is the proportion of offspring that are female (0.5), and S_0 is the annual survival rate of age-0 Burbot (Caswell 2001).

Simulations were used to account for the uncertainty in the fertility and survival rates used to parameterize matrices. The fertility terms used to construct matrices were calculated from randomly generated fertility rates in each simulation. The probability of maturity at each age was generated from a beta distribution (with values constrained to fall between 0 and 1) using the mean and SD equal to the predicted pm_t and SE from the logistic regression of maturity at age (Morris and Doak 2002). Age-specific fecundity was generated in each simulation using a lognormal distribution with mean and SD calculated from fecundity-at-age data (Morris and Doak 2002). Uncertainty in the estimated survival rates was included in the population matrices by generating age-specific survival terms. Estimates of survival rates and their respective SDs were used to generate simulated age-specific survival terms using a beta distribution.

Population growth (λ) was modeled under three management scenarios assuming the high and low estimates of juvenile survival (i.e., S_0, S_1, and S_2). Management scenarios assumed fishing mortality was fully selected for age-1 and older Burbot, age-2 and older Burbot, and age-3 and older Burbot. Each management scenario was maintained for 10 years. The matrix models were not sensitive to starting population size because they did not incorporate density dependence. An estimate of total abundance (N) was unavailable for the Burbot population in the Green River; thus, an arbitrary value of 40,000 individuals was used for modeling. Total abundance was multiplied by the proportion of individuals in each age-class to acquire starting values for population simulation. Age-0–2 Burbot were not fully recruited to the gear; therefore, a linear model was used to predict the abundance of age-0–2 Burbot (Caswell 2000). Each management scenario was simulated 1,000 times using functions from the “popbio” package in R (Stubben and Milligan 2007; R Core Development Team 2014). For each simulation, the population growth rate was computed as $\lambda_t = N_t / N_{t-1}$ over ten 1-year-long time steps and the mean λ_t was calculated over all time steps. The geometric mean of λ_t (λ_G) along with its 95% CI was then calculated to represent the average population growth rate over 10 years (Morris and Doak 2002). The population was assumed to be declining from recruitment overfishing when λ_G was less than 1 (Haddon 2001). Fishing mortality corresponding to the point at which λ_G was less than 1 was used to estimate A for each age-class ($A = 1 - S$). Age-specific estimates of A were averaged to calculate mean total annual mortality.

A sensitivity analysis was conducted to evaluate which age-class most influenced the population growth rate of Burbot in the Green River (Morris and Doak 2002). Commonly applied sensitivity analyses using matrix eigenvalues are concerned with long-term population dynamics (Morris and Doak 2002). However, we were interested in sensitivity over a relatively short time period; thus, a conventional simulation approach was used (Cross and Beissinger 2001). The sensitivity of age-specific survival was calculated as the percent reduction in λ_G over a 10-year time frame given a 10% reduction in the survival rate. Age-specific survival was reduced by 10% while holding all other vital rates constant and replicated through 1,000 matrices. The reduction in λ_G between altered and unaltered matrices was calculated over a 10-year time frame and averaged across the 1,000 replicates. Sensitivities were calculated assuming no fishing mortality.

RESULTS

In total, 568 Burbot were sampled during the summer and autumn. The Burbot varied in length from 52 to 719 mm and had a mean length of 369 mm (Figure 2). In addition, the fish varied in age from 0 to 9 years. Female Burbot were first mature at age 3, which corresponded to a mean length of 341 mm. About 50% of the age-3 and all of the age-8 female Burbot were sexually mature (Table 1). The male Burbot sampled were first mature at age 2, which corresponded to a mean length of 273 mm. Approximately 50% of the age-2 and all of the age-8 male Burbot were sexually mature.

Fecundity increased with length for female Burbot in the Green River (Figure 3). A 350-mm female Burbot had an estimated fecundity of 207,683 ± 41,779 eggs (mean ± SE). The fecundity of a 500-mm female Burbot was estimated to be 677,223 ± 29,523 eggs and that of a 700-mm female Burbot 1,300,146 ± 56,972 eggs.

Assuming low juvenile survival and no fishing mortality, the 10-year estimate of λ_G of Burbot in the Green River was 1.11 (95% CI = 1.09–1.12; Figure 4). When age-1 and older Burbot were targeted for removal, the population dropped below its replacement value when $F = 0.12$. That value of F corresponded to a mean total annual mortality rate (A) of 0.62 for age-1 and older Burbot. When age-2 and older Burbot were suppressed, the population dropped below its replacement value when $F = 0.16$, which corresponded to $A = 0.63$. When age-3 and older Burbot were targeted for removal, the population reached recruitment overfishing when $F = 0.22$, which corresponded to a mean $A = 0.64$. Relative to its value at $F = 0$, A increased by 5% for age-1 and older Burbot, 6% for age-2 and older Burbot, and 7% for age-3 and older Burbot.

In the absence of fishing mortality, the 10-year estimate of λ_G for Burbot in the Green River assuming high juvenile survival was 2.07 (2.04–2.12; Figure 4). When age-1 and older Burbot were fully selected for exploitation, the population growth rate reached recruitment overfishing at $F = 0.43$, which corresponded to a mean $A = 0.70$ for age-1 and older Burbot. The population growth rate dropped below its replacement value at $F = 0.69$ when age-2 and older Burbot were targeted for removal, which corresponded to a mean $A = 0.76$ for age-2 and older Burbot. When age-3 and older Burbot were targeted for removal, the population never reached recruitment overfishing when F varied from 0 to 1.5. Relative to its value at $F = 0$, A increased by 15% for age-1 and older Burbot and 21% for age-2 and older Burbot.

The population growth rate was most sensitive to the survival of age-0 and age-1 Burbot (Figure 5). Assuming low juvenile survival, a 10% reduction in the survival of age-0 Burbot resulted in a 40% reduction in the population growth rate over 10 years. With high juvenile survival, a 10% reduction in the survival of age-1 Burbot produced a 70% reduction in the population growth rate over 10 years.

DISCUSSION

Burbot in the Green River exhibited faster growth than those in other lotic systems. In the Tanana River, Alaska, Burbot averaged 236 mm at age 3 (Chen 1969), whereas age-3 Burbot in the Green River had a mean length of 319 mm. The differences in growth are even more pronounced when the Burbot in the Green River are compared with populations in the southern extent of the species' range. In Torrey Creek, Wyoming, and the Susquehanna River, Pennsylvania, age-2 to age-5 Burbot only grew about 36 mm per year (Robins and Deubler 1955; Miller 1970). Over the same age range, the Burbot in the Green River grew approximately 66 mm per year. These differences in growth are likely due to a number of abiotic (e.g., temperature) and biotic factors (Rose et al. 2001; Quist et al. 2012). The fact that the Burbot in the Green River are growing faster than those in other lotic systems suggests that the Burbot in the Green River have abundant prey resources and are able to maximize somatic growth.

Growth influences the maturity schedule and fecundity of fish in a population (Ferreri and Taylor 1996; Quist et al. 2012). Burbot generally reach sexual maturity around 400 mm (Chen 1969; Pulliainen and Korhonen 1990; Bernard et al. 1993), though age at maturity is highly variable and dependent on individual growth. Evenson (1990) reported that female Burbot in the Tanana River reached sexual maturity at age 6 (498 mm). Burbot in the Susquehanna River reached sexual maturity between ages 3 and 4 (240–265 mm; Robins and Deubler 1955). The majority of the Burbot in the Wind–Bighorn drainage, Wyoming, reached sexual maturity at age 4, but length at maturity varied among water bodies (Hubert et al. 2008). For instance, age-4 Burbot in Trail Lake

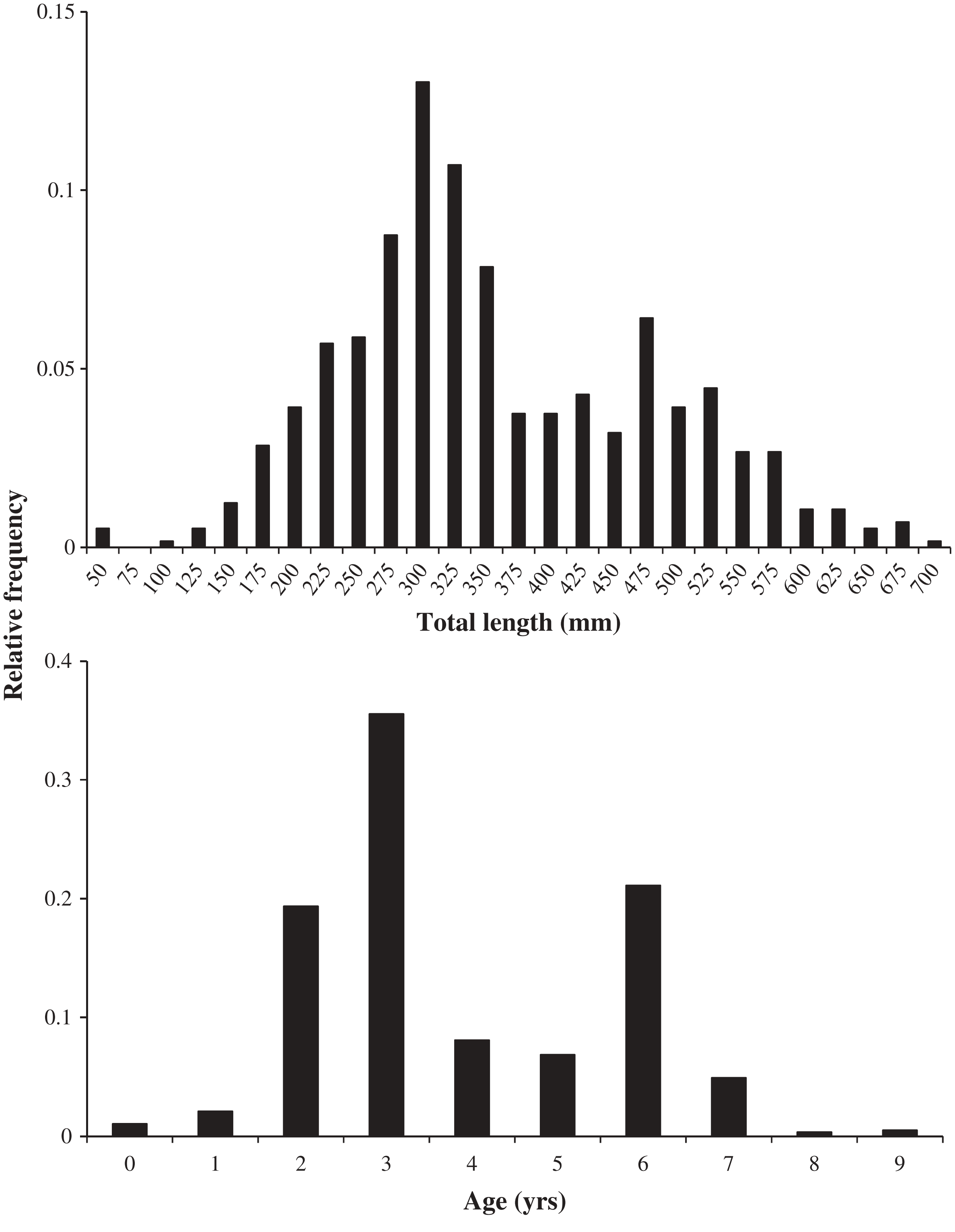

FIGURE 2. Length and age distributions of Burbot sampled in the Green River during the summer and autumn of 2013.

reached maturity at 246 mm, whereas the Burbot in Boysen Reservoir that were sexually mature at age 4 had an average length of 546 mm (Miller 1970). The Burbot in the Green River reached sexual maturity at age 3, which is young compared with the ages at maturity of other populations. The early maturation of Burbot in the Green River is not surprising considering their relatively fast

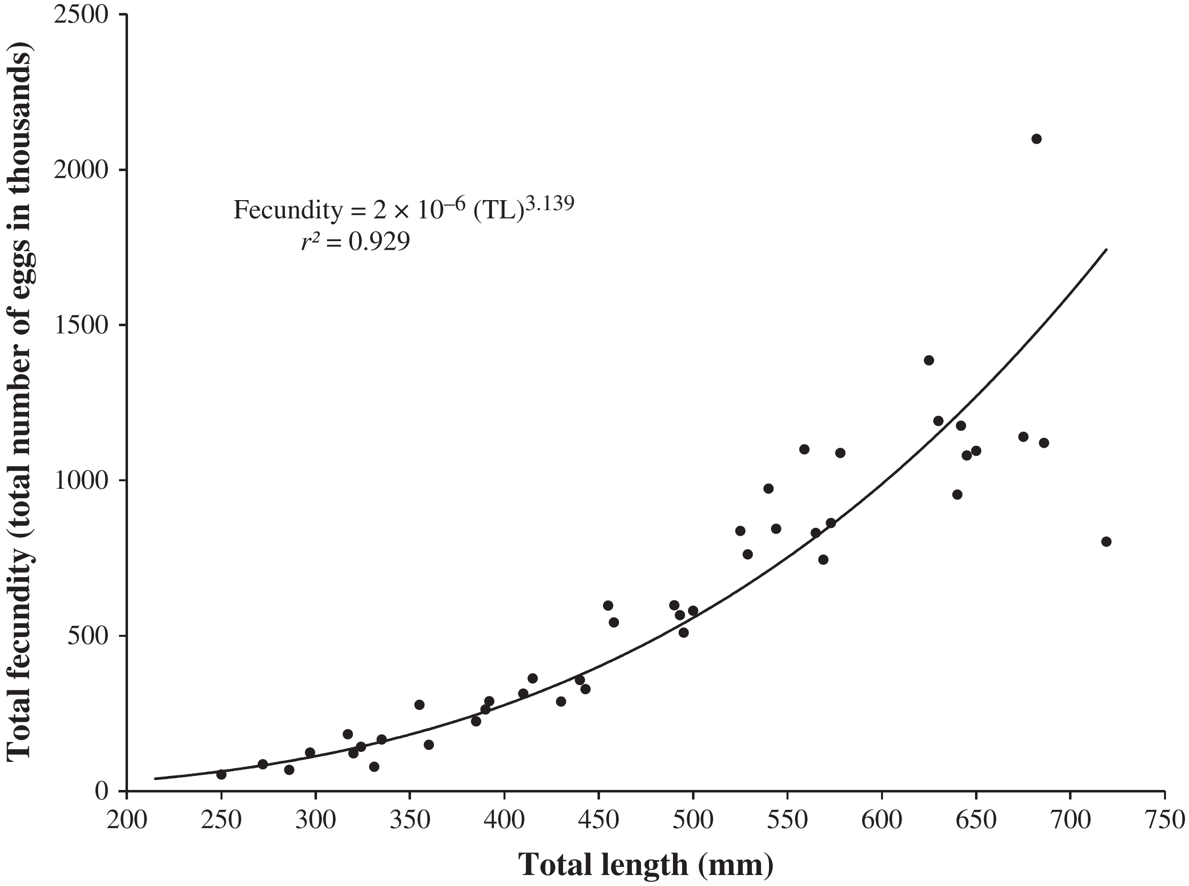

FIGURE 3. Fecundity–length relationship for Burbot sampled from the Green River during the autumn of 2013. The individual dots represent data points, the solid line the fitted regression model.

growth rate. Additionally, Burbot in the Green River were highly fecund, with an average total fecundity of 823,591 eggs per female. Adult Burbot in southwestern Lake Superior averaged 492 mm in length and had a mean fecundity of 812,282 eggs (Bailey 1972). In Lake Hańcza, Poland, adult female Burbot averaged 308 mm in length and had a mean fecundity of 189,400 eggs (Brylinska et al. 2002). Roach and Evenson (1993) estimated the total fecundity of Burbot from the Tanana River and found that female Burbot with a mean length of 703 mm have an average fecundity of 969,986 eggs. The fact that the Burbot in the Green River matured early and were highly fecund suggests that they can obtain the energy necessary for high reproductive output.

Our age-structured population model indicated that the Burbot population in the Green River will likely increase under current conditions. However, the estimated population growth rates are based on a number of assumptions that may not reflect the true state of the Burbot population in the Green River. In particular, changes in survival would substantially influence the population growth rate. Adult survival was estimated from a single year's catch data, which seemed to exhibit variability in recruitment. Although recruitment variability violates one of the assumptions of mortality estimation using the Chapman–Robson estimator, our estimate of mortality is the best estimate available for Burbot in the Green River. The high estimate of age-0 survival used in our population modeling was obtained from a study evaluating larviculture techniques for Burbot (Vught et al. 2008). The authors stocked larval Burbot into earthen ponds following yolk absorption and then evaluated mortality after 9 months. Under natural conditions, Burbot would likely suffer significant mortality during the egg and early larval stages due to biotic (e.g., predation) and abiotic (e.g., water temperature) factors; thus, the high estimates of juvenile survival used in our population modeling likely overestimated the true population growth rate. Paragamian and Laude (2009) also evaluated the survival of hatchery-reared juvenile Burbot in earthen ponds; however, Yellow Perch *Perca flavescens* were accidentally stocked into the pond and caused high mortality of juvenile Burbot. The high juvenile mortality reported by Paragamian and Laude (2009) may be more similar to that of the Burbot in the Green River, which are subject to predation. Thus, estimates of the population growth rate using low survival may better represent the population growth of the Burbot in the Green River. An additional assumption that may not be realistic is that of spawning frequency. Our

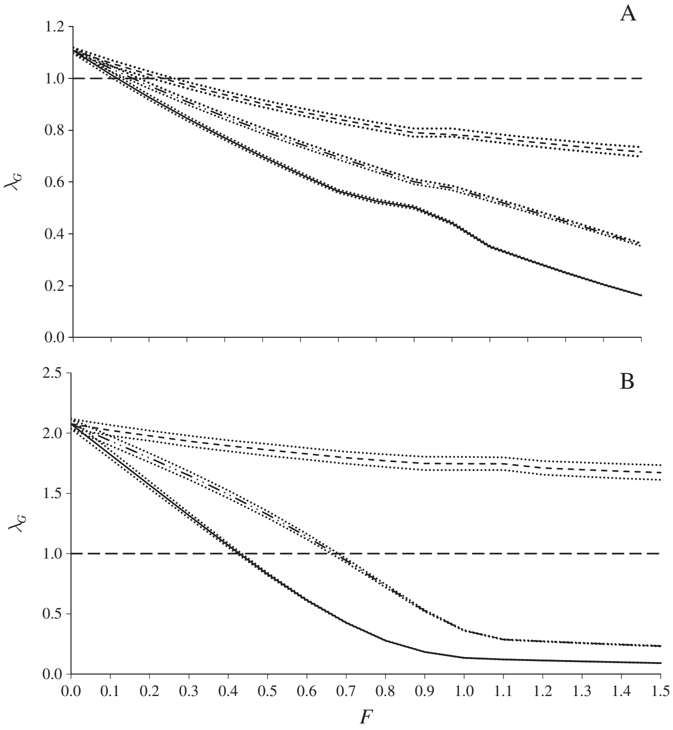

FIGURE 4. Population growth rates (λ_G) over a 10-year time frame for Burbot sampled from the Green River during the summer and autumn of 2013. Growth rates were calculated assuming **(A)** low and **(B)** high survival (see text) of age-0–2 Burbot and fully selected fishing mortality (*F*) for age-3 and older Burbot (short-dashed line), age-2 and older Burbot (dotted–dashed line), and age-1 and older Burbot (solid line). The dotted lines represent 95% confidence intervals, and the horizontal dashed line at λ_G = 1 denotes the replacement value.

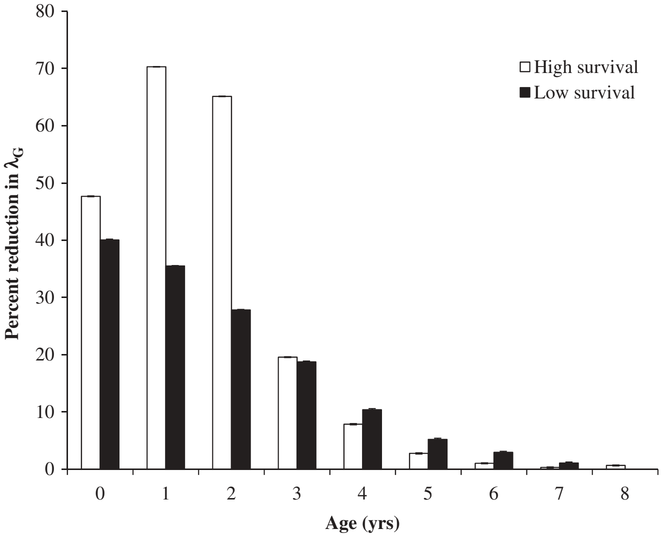

FIGURE 5. Percent reductions in geometric means of the population growth rate (λ_G) given 10% reductions in age-specific survival assuming high juvenile survival and low juvenile survival for Burbot in the Green River sampled during the summer and autumn of 2013. Error bars represent SEs. The reductions in the population growth rate for age-9 Burbot were less than 0.001% and are therefore not displayed.

population model assumed a worst-case scenario in which all of the mature female Burbot spawned every year. In reality, the spawning frequency of Burbot is highly variable, with reports varying from 60% to 95% in a given year (Evenson 1990; Pulliainen and Korhonen 1990, 1993). Any reduction in the current spawning frequency of Burbot in the Green River would ultimately result in a decrease from the current estimated population growth rate. Regardless of the uncertainties in model inputs, population metrics (e.g., age structure, age at maturity, and total fecundity) suggest that without intervention Burbot will persist in the Green River.

The age-structured population model indicated that the Burbot population in the Green River would require substantial levels of exploitation to reduce the population growth rate below the replacement value ($\lambda_G < 1$). For example, achieving recruitment overfishing assuming that only age-3 and older Burbot were removed (and low survival) would require an $A = 0.58$. The total annual mortality rate needed to cause recruitment overfishing of Burbot in the Green River is similar to the levels of mortality required to suppress other nonnative fishes. Simulations for nonnative Lake Trout in Lake McDonald, Montana, indicate that recruitment overfishing would occur when *A* was between 0.44 and 0.49 (Dux 2005). Similarly, Barbour et al. (2011) evaluated the potential removal of nonnative Red Lionfish *Pterois volitans* from the western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico and concluded that an *A* of at least 0.60 would be needed to cause recruitment overfishing. Hansen et al. (2010) estimated that an *A* between 0.45 and 0.50 would be required to reduce the number of nonnative Lake Trout to below the replacement value in Lake Pend Oreille, Idaho. Though possible, the cost associated with achieving high annual mortality rates represents a substantial economic investment. In Lake Pend Oreille alone, it costs approximately US$400,000 annually to deploy trap and gill nets targeting nonnative Lake Trout (Martinez et al. 2009). Similarly, large-scale predator removal and prevention programs focused on recovering native fishes in the Colorado River were estimated to cost $1,400,000 annually in 2000 (Mueller 2005). Given the considerable cost associated with suppressing fish populations, any effort to increase the efficiency of removal efforts is beneficial to natural resource management agencies.

Sensitivity analysis indicated that the population growth rate of the Burbot in the Green River was most sensitive to the survival of age-0 and age-1 fish. Our results are similar to those reported by previous researchers. For example, Worthington et al. (2011) reported that population persistence was independent of spawning frequency when juvenile survival was high (0.15%). In addition, these authors noted that a reduction in juvenile Burbot survival (to 0.002%) would require an increase in annual spawning frequency to ensure population persistence. Our results indicate that targeting age-0 and age-1 Burbot would cause the greatest reduction in the population growth rate over 10 years. However, targeting younger age-classes using established methods (e.g., hoop nets, electrofishing) may be difficult. For example, age-1 Burbot accounted for only about 4% of the total Burbot in our sample. It is unclear whether these results are indicative of low capture efficiency or low densities of juvenile Burbot in the study area. Fisher (2000) reported that age-0 and age-1 Burbot used backwater habitats in the Missouri River, North Dakota. Additionally, Dillen et al. (2008) reported that larval and fingerling Burbot were sampled exclusively in tributaries of lowland rivers in France. Only the main channel of the Green River was sampled in our study; thus, the low number of Burbot sampled may be the result of differential habitat use by juvenile and adult Burbot. Nevertheless, future research should attempt to identify effective sampling techniques for juvenile Burbot and evaluate size-specific habitat use by Burbot.

An additional option to improve the suppression of Burbot in the Green River is to increase angler exploitation. Angler harvest is commonly used by resource management agencies to control or reduce the total abundance of fishes (Mueller 2005; Hansen et al. 2010). Angler exploitation is often hypothesized as the cause of declining Burbot populations within the species' native distribution (Hubert et al. 2008; Stapanian et al. 2010) and represents an inexpensive option for controlling Burbot in the Green River. In fact, angler exploitation has been employed in Flaming Gorge Reservoir to control the abundance of Burbot. Since 2010, anglers have removed over 23,000 Burbot from that reservoir (Wyoming Game and Fish Department 2014). However, this removal effort is the result of the annual "Burbot Bash" fishing derby in which cash prizes are awarded for angled Burbot. Similar incentives have been used in other systems to increase the harvest rate of nonnative fishes. In Lake Pend Oreille, angler exploitation of Lake Trout had a significant influence on population growth only after a $15/fish bounty was instituted (Martinez et al. 2009). Currently, few anglers target Burbot on the Green River; however, an angler incentive program may increase angler exploitation. Although anglers would likely only harvest large, adult Burbot, any increase in angler exploitation would contribute to the control of Burbot in the Green River, ultimately reducing the overall cost of removal efforts.

Another option for controlling the distribution and abundance of Burbot in the Green River is to target spawning aggregations. In an effort to maximize removal rates, spawning sites of mature nonnative Lake Trout are routinely targeted in lakes of the western United States (Martinez et al. 2009; Dux et al. 2011). Aggregations of Common Carp *Cyprinus carpio* have been identified using telemetry in Clear Lake, Iowa, to inform removal efforts (Penne and Pierce 2008). Bajer et al. (2011) targeted winter aggregations of Common Carp in Lake Gervais, Minnesota, and were able to remove approximately 52% of the population in a single day of seining. In lotic systems, Burbot commonly form "spawning balls" in low-velocity areas during the winter, often under ice (Sorokin 1971; Breeser et al. 1988; McPhail and Paragamian 2000). Spawning aggregations represent high densities of Burbot which, if targeted, may increase the efficiency of physical removal and reduce the overall cost of suppression.

Our results indicate that the Burbot in the Green River grow relatively quickly, mature early, and have high fecundity. In addition, the results from our age-structured population model indicate that the Burbot population in the Green River will likely grow without intervention. Despite their exponential population growth, the successful suppression of Burbot in the Green River is likely tenable. However, prior to implementing a large-scale suppression program, research should attempt to fill the knowledge gaps associated with the vital rates used for population modelling, particularly juvenile survival. Additionally, the difficulty associated with efficiently sampling Burbot necessitates further research into effective removal strategies. Angler exploitation and targeting spawning aggregations represent two options to increase the efficiency of removal efforts, but by no means do they represent an exhaustive list. Therefore, future research should attempt to identify novel strategies for effectively removing Burbot in the Green River system.

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