Population Characteristics, Movement Dynamics, and Management of Nonnative

Burbot in the Green River System, Wyoming

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by

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Authorization to Submit Thesis

This thesis of Tucker A. Brauer, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Population Characteristics, Movement Dynamics, and Management of Nonnative Burbot in the Green River System, Wyoming," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Suppression programs targeting undesirable fish species are difficult and effort intensive,

often requiring substantial effort by management agencies. Before suppression programs can

be implemented, it is necessary to gain an in-depth understanding of the invader's ecology to

increase the effectiveness of removal efforts. This is especially true in the Green River

system, Wyoming, where invasive Burbot have the potential to negatively influence native

fishes and socially important fisheries. This thesis evaluated the efficacy of using angling data

to monitor invasive Burbot *Lota lota* populations in the Green River basin and described the

potential response of Burbot populations to various management scenarios. In addition, I

evaluated the movement dynamics of Burbot in the Green River. My research suggests that

angler-supplied Burbot are a cost-effective data source for monitoring Burbot populations.

Results indicate that exploitation of mature Burbot must reach 33% to suppress lentic portions

of the Green River Burbot population. Additionally, adfluvial Burbot in the upper Green

River system seem to spawn near Fontenelle Reservoir. Focusing removal effort on this

portion of the Green River could increase the efficiency of a suppression program.

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Chapter 1: General Introduction

The introduction of nonnative fishes outside their natural distributions has substantially altered freshwater communities worldwide (Pysek and Richardson 2010). When introduced outside their native distribution, nonnative species often affect native fish populations through competitive interactions, hybridization, predation, habitat alteration, or as disease vectors (White and Harvey 2001; Taniguchi et al. 2002; Chornesky and Randall 2003; Miller and Crowl 2006; Poulin et al. 2011). For instance, the decrease in native Yellowstone Cutthroat Trout *Onchorhynchus clarkii bouvieri* populations in Yellowstone Lake, Wyoming, during the past two decades is largely related to predation by nonnative Lake Trout *Salvelinus namaycush* and the effects of the exotic parasite *Myxobolus cerebralis* (Ruzycki et al. 2003; Koel et al. 2005). When a species is introduced, becomes established, and poses an ecological, economical, or health threat to native species, those species are deemed invasive and warrant management action (NISC 2001).

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 is established, suppression or eradication become the best possible options to mitigate their possible negative effects on native fauna (Kolar et al. 2010). Suppression programs are expensive and difficult, requiring more expense and effort than is often feasible (Chornesky and Randall 2003; Mueller 2005; Quist and Hubert 2004). 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 (Simberloff 2003). The current situation involving invasive Burbot *Lota lota* in the Green River of Wyoming is one such example.

Burbot is the only freshwater representative of the cod family (i.e., Gadidae), and has a circumpolar distribution extending throughout northern Europe, Asia, and portions of North America (McPhail and Paragamian 2000). Adult Burbot are top predators, aggregate spawners, and exhibit multiple life history strategies throughout their distribution (Hewson 1955; McPhail and Paragamian 2000). The conservation status of Burbot is highly variable. A status review by Stapanian et al. (2010) showed that Canadian populations are generally stable. Only four of twenty-four countries in Europe and Asia reported secure populations of Burbot, the remainder reported Burbot populations as vulnerable, declining, imperiled, or extirpated. Similarly, only eight of twenty-five states in the United States claimed secure populations (Quinn 2000; Stapanian et al. 2010). The poor status of Burbot in their native distribution has prompted a focus on their conservation (Ireland and Perry 2008; Stapanian et al. 2010; Neufeld et al. 2011; Paragamian and Hansen 2011). Invasive Burbot populations elicit a different management response which is generally focused on population control. Such a dissimilarity in management objectives can be observed in Wyoming.

Burbot are native to Wind-Big Horn and Tongue river basins of Wyoming (Baxter and Stone 1995). They have been extirpated from the Tongue River system and occur at low densities in the Wind-Big Horn River drainage (Krueger and Hubert 1997; Hubert et al 2008; Underwood et al. 2016). Their status has prompted their classification as a "species of greatest conservation concern" in these systems (WGFD 2017). Conversely, Burbot were illegally introduced in the Green River basin in the 1990s (Gardunio et al. 2011). Due to the potential of Burbot to alter the structure of the Green River system (Klobucar et al 2016; McBaine et al. *in press*), Burbot have been labelled as a "significant and immediate threat" to native species as well as economically, socially, and ecologically important sport fisheries (WGFD 2017).

In response to the possible negative effects of Burbot to fishes in the Green River basin, the Wyoming Game and Fish Department (WGFD) has begun exploring the efficacy of a suppression program targeting Burbot. Prior research in the system suggested that high total annual mortality ($> 60\%$) is needed to effectively suppress Burbot in the Green River (Klein et al. 2016). However, this estimate was based on estimates derived from riverine Burbot and did not include data from reservoir populations of Burbot. Due to potential differences in demographics between lotic and lentic populations of Burbot, the applicability of the current riverine-specific population model in reservoir habitats is unknown. Previous research also suggests that Burbot in the Green River system may be exhibiting an adfluvial life history (Klein et al. 2015). Burbot are known to travel long distances in rivers to spawn elsewhere in their distribution (Evenson 1993; Paragamian 2000; Schram 2000). If long-distance movements are occurring in the Green River system, those movements could increase the probability of negative interactions with important fisheries located in the upper Green River. Understanding the movement patterns of Burbot and identifying potential spawning locations in the Green River has also been suggested as a means to increase the effectiveness of proposed suppression efforts (Klein et al. 2016). Additionally, high costs associated with suppression programs warrants the development of cost-effective methods to monitor the response of fish populations to management actions. Using various Burbot tournaments on reservoirs in the Green River system as a data source for monitoring could reduce the costs of suppression efforts.

Considering the sizeable gaps in knowledge regarding the efficacy of a removal program targeting Burbot, this thesis had three main objectives. The first objective was to evaluate the efficacy of using angler-supplied data to monitor the Burbot population in the

Green River system. Secondly, the population demographics and potential response of reservoir Burbot populations to management effort were evaluated using an age-structured population model. Lastly, the movement dynamics of Burbot in the upper Green River were described to increase the efficacy of a removal program.

Thesis Organization

This thesis is composed of five chapters. The second chapter evaluates differences in the vital rate estimates gleaned from fishery-dependent and fishery-independent data sources to evaluate the efficacy of using angler-supplied data to monitor Burbot populations in the Green River system. Chapter two has been submitted for publication in the *North American Journal of Fisheries Management*. The third chapter describes the demographics of lentic populations of Burbot in the Green River system and evaluates their potential response to various management scenarios. Chapter 3 has been submitted for publication in the *North American Journal of Fisheries Management*. Chapter 4 evaluates the movement dynamics of Burbot in the upper Green River system and has been submitted to the *North American Journal of Fisheries Management*. The final chapter provides general conclusions and describes the management implications of chapter results.

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Chapter 2: Efficacy of Using Data from Angler-Caught Burbot to Estimate Population Rate Functions

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Abstract

The effective management of a fish population depends on the collection of accurate demographic data from that population. Since demographic data is often expensive and difficult to obtain, developing cost effective and efficient collection methods is a high priority. This research evaluates the efficacy of using angler-supplied data to monitor a nonnative Burbot *Lota lota* population. Age and growth estimates were compared between Burbot collected by anglers and in trammel nets from two Wyoming reservoirs. Collection methods produced different length-frequency distributions, but no difference was observed in age-frequency distributions. Mean back-calculated lengths at age revealed that netted Burbot grew faster than angled Burbot in Fontenelle Reservoir. In contrast, angled Burbot grew slightly faster than netted Burbot in Flaming Gorge Reservoir. Von Bertalanffy growth models differed between collection methods, but differences in parameter estimates were minor. Estimates of total annual mortality (A) of Burbot in Fontenelle Reservoir were comparable between angled ($A = 35.4\%$) and netted fish (33.9%); similar results were observed in Flaming Gorge Reservoir for angled (29.3%) and netted fish (30.5%). Beverton-Holt yield-per-recruit models were fit using data from both collection methods. Estimated yield differed by less than 15% between data sources and reservoir. Spawning potential ratios indicated that an exploitation rate of 20% would be required to induce recruitment overfishing in either reservoir, regardless of data source. Results of this study suggest that angler-supplied data are

useful for monitoring Burbot population dynamics in Wyoming and may be an option to efficiently monitor other fish populations in North America.

Introduction

Population demographic data are the basis of fisheries management as they provide insight on the recruitment dynamics, trophic interactions, and growth of fish populations (Allen and Hightower 2010; Quist et al. 2012). Accurate data on fish population dynamics are important for monitoring sport fish populations and especially critical for monitoring introduced fish populations prior to and in response to removal efforts (Cambray 2003). Because collecting demographic data is expensive and time consuming, developing cost-effective techniques is a high priority. A potential cost-effective technique to monitor populations is to use information from angler-caught fish.

Management agencies often employ anglers to gather data on fish populations and to monitor angler effort and harvest (Willis and Hartmann 1986; Dolman 1991; Cooke et al. 2000; Park 2007). Angler-catch data provide an alternative to fishery-independent data (e.g., standard population surveys) used by natural resource agencies. For example, Travnicheck and Clemons (2001) used long-term data from fishing tournaments to evaluate changes in Flathead Catfish *Pylodictis olivaris* populations after closure of commercial harvest in the Missouri River. Ebbers (1987) found that age-frequency distributions, growth rates, and mortality rates estimated for Largemouth Bass *Micropterus salmoides* in Minnesota lakes were similar between angler-supplied data and electrofishing surveys. In contrast, a number of studies suggest that fishery-dependent data should be used with caution. Gabelhouse and Willis (1986) concluded that biases related to angling technique (e.g., gear size and type) and season limited the use of data from Largemouth Bass tournaments in Kansas. Similarly,

Miranda et al. (1987) found that angler-catch data tended to overestimate Largemouth Bass growth rates when compared to data collected using standard survey methods (i.e., electrofishing, cove rotenone). Substantial length bias in angler-supplied data has also been reported in crappie *Poxomis* spp. (Miranda and Dorr 2000) and Northern Pike *Esox lucius* (Arlinghaus et al. 2008) populations. The majority of studies that have investigated the use of angler-catch data have focused on popular sport fishes. Although less common, anglers that target introduced species have the potential to provide valuable information at a fraction of the cost of standard monitoring regimes. Angling tournaments targeting illegally introduced Burbot *Lota lota* in the Green River basin of Wyoming provide an excellent opportunity to evaluate whether data from angling can be used to monitor fish populations.

Burbot are top predators, aggregate spawners, and occupy a diversity of lotic and lentic habitats (Hewson 1955; McPhail and Paragamian 2000). Throughout their native distribution in Wyoming, Burbot populations are in decline or have been extirpated (Krueger and Hubert 1997; Hubert et al 2008; Stapanian et al. 2010). Despite poor status in their native distribution, a population established through illegal introduction is thriving in the Green River basin. The presence of Burbot in the Green River system is a concern due to their potential negative effects on socially and economically important fishes (Gardunio et al. 2011). In response, the Wyoming Game and Fish Department (WGFD) has implemented regulations in the Green River basin that are designed to maximize fishing mortality. The WGFD is also investigating the efficacy of suppression programs (Klein et al. 2015a, 2015b, 2016). Anglers have become interested in participating in suppression efforts and have organized multiple ice-fishing tournaments for Burbot on Fontenelle and Flaming Gorge reservoirs, the two primary reservoirs in the system. Tournaments were organized as a means

to reduce Burbot numbers and have resulted in the removal of approximately 34,000 Burbot since tournaments began in 2010 (JDW, unpublished information). In addition to their effectiveness as a removal tool, angling tournaments provide fish that can be used to evaluate and monitor Burbot age structure and growth.

Age and growth data are of utmost importance to fishery managers. Age-structure data provide insight on the mortality rates and recruitment dynamics of fish populations. Growth data are especially important because growth has direct and indirect effects on recruitment, mortality, maturity, and length structure of a population (Quist et al. 2012). Given the importance of age and growth data, new sampling methods should be assessed to evaluate concordance with standardized sampling methods. This study was conducted to compare age and growth estimates of Burbot from fishery-dependent (i.e., angler-caught) and independent (i.e., standard trammel netting survey) data sources in two Wyoming reservoirs. Given the results of previous studies addressing this topic, we hypothesized that fishery-dependent data would overestimate growth when compared to estimates from fishery-independent data sources and population models fit to both data types would differ substantially in their results.

Study area

This research took place on Fontenelle and Flaming Gorge reservoirs, both of which are located in the Green River basin, Wyoming. Fontenelle Reservoir is an artificial impoundment of the Green River located in Lincoln County. The reservoir is primarily used for flood protection with a secondary use of hydroelectric power generation. At capacity, the reservoir has a surface area of approximately 3,200 hectares and a maximum depth of approximately 30 meters. Flaming Gorge Reservoir is located 125 km downstream of

Fontenelle Reservoir and is primarily located in Sweetwater County, Wyoming, with the southernmost portion of the reservoir located in Daggett County, Utah (Figure 1). As such, the Flaming Gorge Reservoir fishery is managed by both the WGFD and the Utah Division of Wildlife Resources. The reservoir is primarily used for hydroelectric power generation. At capacity, the reservoir has a surface area of approximately 17,000 hectares and a maximum depth of 133 meters.

Methods

Tournament data were collected from Fontenelle and Flaming Gorge reservoirs during January, 2016 and 2017. Data were collected from one tournament on Fontenelle Reservoir and two tournaments on Flaming Gorge Reservoir. The tournament on Fontenelle Reservoir occurred over one night, whereas tournaments on Flaming Gorge Reservoir each spanned two nights. Tournaments offered cash prizes for the largest Burbot, smallest Burbot, and most Burbot caught by one fishing team. The rules of the competition indicated that all Burbot had to be euthanized and checked in to be eligible for judging.

At each tournament check-in, anglers were informed that a study was being conducted, and the premise of the study was explained. Anglers were invited to donate their catch. Due to logistical constraints, biological data were only collected from donated fish, not from the total tournament catch. Donated fish were enumerated, and total length (mm) and weight (g) were measured. Sex was determined for all fish by visual observation of the gonads. Collection of ovaries from mature female Burbot was attempted, but all had spawned prior to sampling. Sagittal otoliths were taken from up to ten fish per 1-cm length group (Quist et al. 2012; Klein et al. 2014).

Burbot were collected from Fontenelle and Flaming Gorge reservoirs in October and November, 2016, using trammel nets. Trammel nets have been found to be effective at capturing lentic Burbot during spring and fall and have become the standard gear for sampling Burbot in lentic waters in Wyoming (WGFD, unpublished information). Trammel nets measured 48.8 m long, 1.8 m deep and consisted of 25.4-cm bar measure outer mesh and 2.5-cm bar measure inner mesh. Nets were placed perpendicular to shore at varying depths and anchored to the substrate at both ends. Trammel nets were placed in locations used annually by the WGFD during fall Burbot sampling. All netted fish were counted, and total length (mm) and weight (g) were measured. Sex was determined by visual observation of the gonads. Ovaries were removed from up to five mature female Burbot per 5-cm length group, preserved in 5% formalin solution, and stored for fecundity analysis. Sagittal otoliths were removed from up to ten fish per 1-cm length group. All otoliths were dried, stored in 2.0 ml centrifuge vials, and returned to the University of Idaho for processing.

Otoliths were mounted in epoxy and transversely sectioned about the nucleus (Koch and Quist 2007; Edwards et al. 2011; Klein et al. 2014). Otolith cross sections were examined using a dissecting microscope with transmitted light and an image analysis system. Otoliths were examined by a single reader that had previous experience ageing otoliths. If an age estimate could not be reached for a fish, that fish was removed from further analyses. Ovaries were blotted dry and weighed to the nearest 0.01 g. One ovary was randomly selected for subsampling. Subsamples of oocytes (0.01-0.02 g) were taken from the anterior, central, and posterior portions of the ovary. Oocyte subsamples were then counted using a dissecting microscope and an average of subsample counts was calculated. Averages were then used to

determine total fecundities based on total ovary weight (Klibansky and Jaunes 2007; Klein et al. 2016)

Mean back-calculated lengths were estimated using the Dahl-Lea method (Quist et al. 2012). Burbot growth rates were described using a von Bertalanffy growth model:

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

where L_t (mm) is length at time t, L_∞ is average maximum length, k is growth coefficient, and t_o is the theoretical age when length is zero (Quist et al. 2012). All analyses were conducted using the "FSA" package in R version 3.2.2 (R core development team; Ogle 2015). Proportional size distribution (PSD) was calculated for each reservoir and collection method (Gabelhouse 1984; Fisher et al. 1996; Neumann et al. 2012). Total annual mortality (A) was calculated using a Chapman-Robson estimator and peak plus one criterion (Smith et al. 2012). Mortality rates were calculated for angled fish using only those fish that were donated by anglers, netted fish mortality rates were calculated using all sampled fish whose ages were assigned using an age-length key (Quist et al. 2012).

Chi-square tests were used to compare length-frequency and age-frequency distributions between collection methods in each reservoir ($\alpha = 0.05$; Neumann and Allen 2007; Ogle 2015). Beverton-Holt yield-per-recruit models were used to describe differences in potential yield and spawning potential ratio (SPR) estimates between data collected by anglers and data collected using trammel nets. Models were constructed using the Fishery Analysis and Modeling Simulator v. 1.64 (FAMS; Slipke and Maceina 2014). Yield-per-recruit models required input parameters of growth, mortality, longevity, and length-weight relationship parameters specific to each collection method and reservoir. Spawning potential ratio calculations required additional parameters including fecundity-length relationship

estimates, a maturation schedule, and estimates of spawning frequency (Table 1). Spawning potential ratio is used to index the influence of fishing on the productivity of a population and is calculated as the ratio of fished to unfished mature eggs that are produced in an average recruit's lifetime. Populations were considered to be experiencing recruitment overfishing when SPR was below 0.20 (Goodyear 1993).

Conditional natural mortality (cm) was held constant at 0.10 in all models. Conditional fishing mortality (cf) was allowed to vary from 0-1.0 in increments of 0.05. An arbitrary initial population of 100,000 individuals was input in each model. Logarithmic length-weight relationship and fecundity-length relationship parameters were estimated from our data using linear regression. Since fecundity-length data were unavailable for angled fish, we used the fecundity-length relationships of netted fish for all simulations. Age at first maturation for females was age 2 in each reservoir based on observed maturity rates. We assumed that females composed 50% of the population. Based on our observations when evaluating oocytes, we assumed that 100% of mature female Burbot spawned annually.

Models were run under a single management scenario that assumed no minimum length limit in either reservoir. Both reservoirs are currently managed with no length restrictions on harvest. Since Burbot smaller than 200 mm were absent from our sample, we used 200 mm as the "minimum length limit".

Results

A total of 515 Burbot was sampled from Fontenelle Reservoir, 376 were collected using trammel nets and 139 were collected by anglers. Otoliths were collected from all angled fish and from 139 fish collected using trammel nets. In Flaming Gorge Reservoir, 417 Burbot

were collected. Of these, 214 were collected by anglers and 203 were collected using trammel nets. Otoliths were collected from all angled fish and 155 netted fish. Ovaries were collected from 35 Burbot from Fontenelle Reservoir and 42 Burbot from Flaming Gorge Reservoir.

Lengths of angled fish in Fontenelle Reservoir varied from 293 mm to 900 mm, whereas netted fish varied in length from 304 mm to 965 mm (Figure 2). Lengths of angled fish in Flaming Gorge Reservoir varied from 218 mm to 858 mm and lengths of netted fish varied from 317 mm to 853 mm (Figure 2). Although length distributions of angled and netted fish were statistically different in Fontenelle Reservoir ($\chi^2 = 16.8$, $df = 4$, $P = 0.002$) and Flaming Gorge Reservoir ($\chi^2 = 15.0$, $df = 4$, $P = 0.004$), proportional size distribution estimates were similar between collection methods in both reservoirs (Figure 2).

Angled fish in Fontenelle Reservoir varied in age from 1 to 11 years whereas ages of netted fish varied from 1-12 years (Figure 3). Ages of Burbot in Flaming Gorge Reservoir varied from 1 to 10 years for angled fish and 2 to 11 years for netted fish (Figure 3). No statistical difference in age distributions were observed between angled and netted fish in Fontenelle Reservoir ($\chi^2 = 13.4$, $df = 11$, $P = 0.27$) or Flaming Gorge Reservoir ($\chi^2 = 12.0$, $df = 10$, $P = 0.29$). Estimates of total annual mortality of Burbot in Fontenelle Reservoir were comparable between angled ($A = 35.4\%$) and netted fish (33.9%). Mortality rates in Flaming Gorge Reservoir were also similar between angled (29.3%) and netted fish (30.5%).

Mean back-calculated lengths of Burbot in Fontenelle Reservoir were larger in angled fish than netted fish up to age 5. After age 5, back-calculated lengths of netted fish were larger than angled fish. Conversely, back-calculated lengths of Burbot in Flaming Gorge Reservoir were similar between angled and netted fish until age 3; thereafter, growth of angled fish was

faster than netted fish (Table 2). Parameter estimates from von Bertalanffy growth models differed between collection methods for both reservoirs, but differences were minor (Table 1).

Yield-per-recruit models produced similar estimates using data from angled and netted fish in each reservoir (Figure 4). Burbot sampled with trammel nets in Fontenelle Reservoir had higher potential yield than angled fish. The opposite pattern was observed in Flaming Gorge Reservoir where angled fish had higher potential yield than netted fish regardless of management scenario. Although estimates of yield differed between collection methods, differences in estimated yield varied from 1% to 21% and were generally under 15%. Spawning potential ratio estimates remained consistent between collection methods (Figure 4). Using either data source, models without a minimum length limit indicated that recruitment overfishing would be achievable at an exploitation rate of 20% in both Fontenelle Reservoir and Flaming Gorge Reservoir.

Discussion

The results of this research support our hypothesis that fishery-dependent data would produce different estimates of growth when compared to fishery-independent data. However, a clear pattern was not evident. Miranda et al. (1987) found that back-calculated lengths of angled Largemouth Bass were greater than those collected using cove rotenone and electrofishing. The authors also observed that growth rates converged as fish age increased, suggesting that angling selects for the fastest growing members of younger age classes. In our study, angled fish had larger back-calculated lengths at age than netted fish in Flaming Gorge Reservoir and the opposite pattern was observed in Fontenelle Reservoir. Contrary to our initial hypothesis, the disparity in mean back-calculated lengths between collection methods

was large enough to be statistically significant, but yield-per-recruit models resulted in minor differences in potential yield and SPR estimates between data sources in both reservoirs.

Like many collection methods, angling is size selective. Angling data can also be biased by differences in angling technique, gear type, and species. Miranda and Dorr (2000) found that angler exploitation was highest in intermediate length classes of crappie throughout five Mississippi reservoirs due to factors such as fish behavior and gear type. Schultz (2004) stated that exploitation rates of White Bass *Morone chrysops* were highest in large length-classes in Kansas reservoirs. Similarly, Isermann et al. (2005) detected selective harvest of large Yellow Perch *Perca flavescens* by anglers in comparison to trap-net samples. Although length-frequency distributions differed significantly between collection methods in our study, proportional size distribution values were similar between collection methods. Similarities in proportional size distributions may be an artifact of the manner that the Burbot were collected. Many angling tournaments have size and total weight-based prize payouts (Wilde et al. 1998), and competitive anglers often target large numbers of smaller, scoring-size fish in order to maximize total weight instead of targeting larger, warier fish (Holbrook 1975). This phenomenon was documented by Gabelhouse and Willis (1986) where the size and number of Largemouth Bass caught and reported by tournament anglers relied on the angler's intentions and values during that tournament. The authors found that non-tournament anglers caught size classes that were proportional to those sampled by electrofishing. However, tournament angler catch underestimated the proportional size distributions of small size classes and overestimated those of larger size classes. It is important to consider that anglers in our study were required by law to harvest all captured Burbot. Anglers were also required to present all captured fish to tournament officials as prizes were based on concurrent size and total catch

categories. Such regulations allowed for the collection of small and large size-classes and reduced likelihood of common bias-inducing angler practices (i.e., culling small fish). However, a potential source of bias remains as anglers generally target Burbot in spawning aggregations during tournaments and have a higher chance of catching large, mature fish. Given the similarity in age distributions between data types, this did not seem to be occurring.

Angler data present the opportunity to estimate other population vital statistics such as mortality rates that require reliable age-frequency data. Ebbers (1987) concluded that estimates of total annual mortality for Largemouth Bass in Minnesota were consistent between electrofishing data and tournament-angler-supplied data. The mortality rates in our study were not estimated from total angler catch due to either logistical limitations (e.g., too many fish were caught to process in a timely manner) or angler value limitations (e.g., unwillingness of anglers to donate fish). Therefore, we could not properly estimate age structure for the entire tournament catch. Despite this shortcoming, age-frequency distributions were similar between collection methods in each reservoir in our study. Due to the similarities in age frequencies, estimates of total annual mortality were nearly identical between angled and netted fish. In the future, collecting length data from the entire tournament catch, in addition to collecting otoliths, may provide better insight into the concordance of age structure and mortality estimates derived from angling and netting.

Angling tournaments provide a cost-effective option for monitoring fish populations as well as a removal tool that provides angler opportunity. Kansas' black bass tournament monitoring program has been in place since 1977 and has successfully used angling-tournament data to monitor Largemouth Bass populations and assess management actions (Willis and Hartmann 1986). Similar programs that use angling data as a monitoring tool have

existed in Texas (Dolman 1991), Nova Scotia (Macmillan et al. 2002), and Australia (Park 2007). Successful use of angling data in prior research coupled with the results of this research are promising to fishery managers. Data collected from tournaments produced similar estimates of proportional size distribution, age structure, and total annual mortality to data collected using trammel nets. Estimates of growth varied between collection methods, but yield-per-recruit models fit using both data sources showed minimal difference in their model output. Thus, management decisions (e.g., exploitation targets) would not likely differ based on either data source. Collecting data from tournaments also required substantially less effort than standard survey methods. Trammel netting surveys required approximately one week of intensive netting in each reservoir during which a crew of over ten people using various boats and other equipment (e.g., nets) to collect data. Angling-data collection required one day of collection in Fontenelle Reservoir and two days of collection in Flaming Gorge Reservoir. At tournaments, data collection required minimal equipment and three people to process fish.

We acknowledge that the small sample of tournaments from which we collected data may be a source of bias due to factors such as annual variations in fish abundance and (or) angler behavior. Despite this concern, we argue that the lack of research evaluating angler-supplied data makes the results of our study extremely important to fishery managers. Additionally, the few studies that have compared data sources have focused on a single system; whereas, our study compares data from two dissimilar reservoirs. Given these caveats, occasional comparison with fishery-independent data seems prudent if angler-supplied data are used to monitor populations in the future. Additionally, developing specific

benchmarks for acceptable differences between fishery-dependent and fishery-independent data will be important for fishery managers using angler-supplied data.

Acknowledgements

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Table 2.1. Parameter estimates used in population simulations of Burbot collected by anglers and using trammel nets in Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming (2016 and 2017).

		Collection method			
Variable	Description	Angled	Netted	Angled	Netted
		Fontenelle Reservoir		**Flaming Gorge Reservoir**	
b_{lw}	Slope of regression weight on length[a]	2.886	2.845	3.000	3.127
a_{lw}	Intercept of regression weight on length[a]	-4.968	-4.831	-5.270	-5.636
b_{fec}	Slope of regression fecundity on length[a]	2.693	2.693	3.287	3.287
a_{fec}	Intercept of regression fecundity on length[a]	-1.760	-1.760	-3.405	-3.405
L_{∞}	Theoretical mean maximum length (mm)	1178	1591	2100	2096
k	Growth coefficient	0.091	0.066	0.042	0.036
t_0	Theoretical time when length is zero (years)	-2.815	-1.818	-1.951	-2.771
Age_{max}	Maximum age of sampled fish (years)	11	12	10	11

[a] Independent and dependent variables were $\log_{10}$ transformed

Table 2.2. Mean back-calculated lengths at age for Burbot collected by angling (angled) and using trammel nets (netted) from Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming (2016 and 2017). Standard errors for estimates are included.

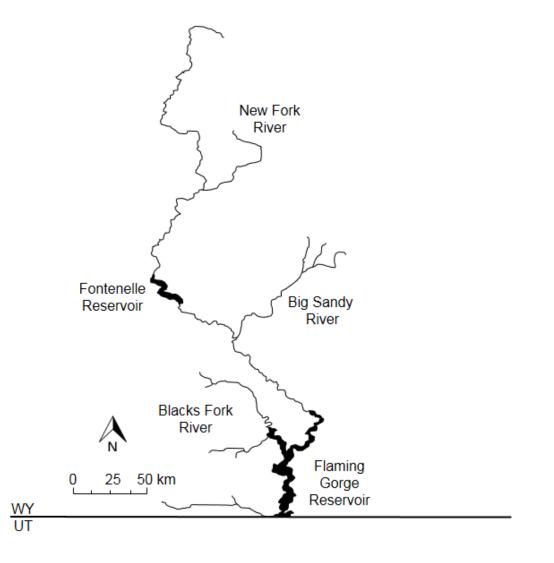| Age	*n* (angled)	*n* (netted)	Angled	*SE*	Netted	*SE*
			Mean back-calculated length at age (mm)			
Fontenelle Reservoir						
1	2	2	251.5	10.2	200.1	12.7
2	3	5	356.7	13.3	317.5	10.1
3	47	55	393.3	3.8	408.2	3.9
4	37	17	512.8	4.5	504.3	6.6
5	13	18	570.8	6.7	568.5	8.9
6	4	9	611.7	18.4	624.8	14.5
7	14	15	659.6	9.3	682.2	10.3
8	8	8	714.8	11.5	761.3	6.6
9	6	5	770.9	13.8	802.1	7.5
10	4	2	818.9	16.5	852.6	4.8
11	1	2	880.5	0.0	878.9	2.1
12	0	1			911.6	0.0
Flaming Gorge Reservoir						
1	15	0	189.9	3.0		
2	28	18	282.3	4.7	289.5	8.7
3	31	19	367.2	5.3	362.9	11.9
4	41	24	448.7	4.6	427.3	12.4
5	24	33	516.9	6.1	490.7	10.2
6	23	24	585.6	6.1	553.6	10.6
7	26	21	645.9	5.4	613.2	9.6
8	13	10	695.8	7.5	665.2	13.7
9	8	4	745.5	9.3	717.8	21.5
10	5	1	803.9	0.0	786.6	40.5
11	0	1			838.5	0.0

Figure 2.1. Map of the Green River basin including its major tributaries and associated reservoirs. Burbot were sampled from Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, during 2016 and 2017.
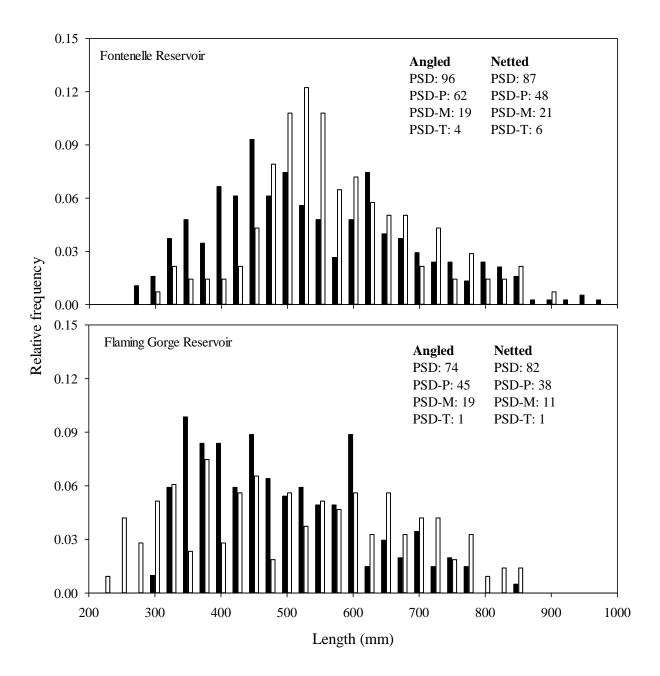
Figure 2.2. Length-frequency distributions of Burbot sampled by anglers (white bars) and trammel nets (black bars) in Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming (2016 and 2017). Proportional size-distributions are provided for stock (PSD), preferred (PSD-P), memorable (PSD-M), and trophy (PSD-T) size classifications.
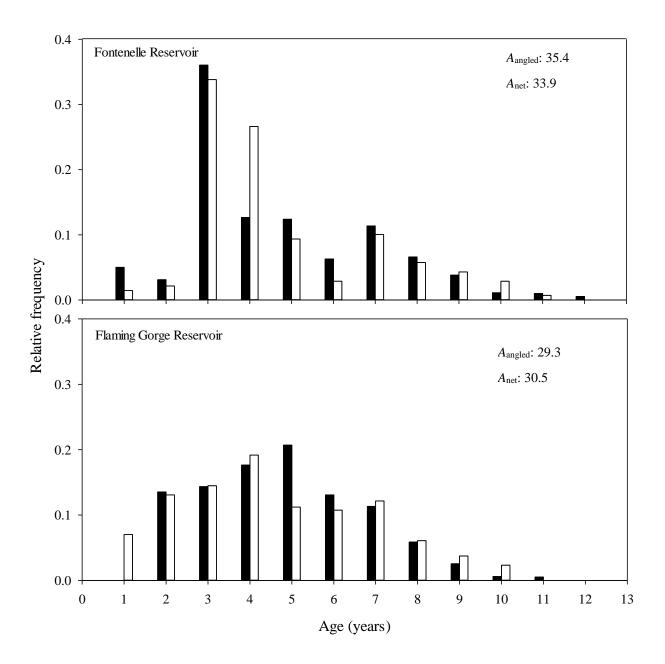
Figure 2.3. Age-frequency distributions of Burbot sampled by anglers (white bars) and trammel nets (black bars) in Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming (2016 and 2017). Variable A represents total annual mortality rate by collection method.
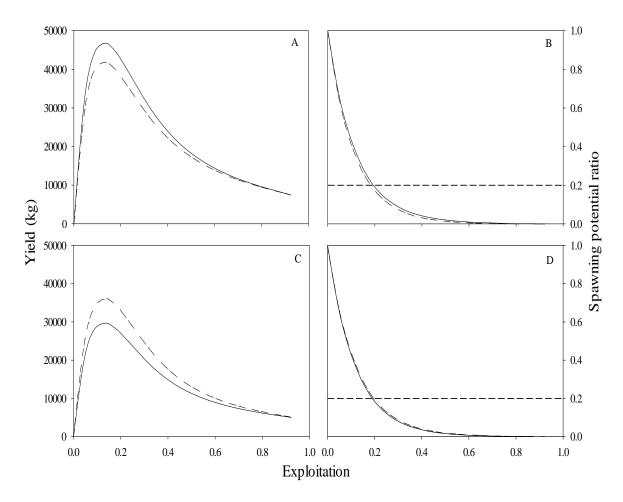
Figure 2.4. Yield-per-recruit models and spawning potential ratios using data collected by anglers and trammel nets. Models included data from: Burbot caught by anglers and assuming no minimum-length limit on harvest (dashed line), Burbot caught using trammel nets assuming no minimum-length limit on harvest (solid line). Panels A and B correspond to fish collected in Fontenelle Reservoir and panels C and D correspond to fish collected from Flaming Gorge Reservoir. Horizontal dashed lines represent the theoretical point where a fishery starts to experience recruitment overfishing.

Chapter 3. Population Characteristics and Management of Lentic Populations of Nonnative Burbot in the Green River System, Wyoming

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Abstract

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. In response to this invasion, managers of the Green River have begun to explore the efficacy of a suppression effort targeting Burbot. 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 for fish in the Green River. Total annual mortality rates of Burbot were approximately 10% lower in reservoirs (33%) than for fish in the Green River. Additionally, reservoir-dwelling Burbot matured earlier than Burbot in riverine environments. An age-structured population model indicated that Burbot populations were growing rapidly ($\lambda = 1.18$) in the study reservoirs. Annual exploitation 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 population growth rate. Focusing removal effort on mature Burbot may be the best and most realistic option for suppressing Burbot populations in the Green River system.

Introduction

Burbot *Lota lota* are the only freshwater representative of the cod family (i.e. Gadidae). They have a circumpolar distribution that rarely extends below 40° N latitude and occupy both lotic and lentic environments throughout their distribution (McPhail and Paragamian 2000). Burbot are a top predator and prey on a variety of fishes and invertebrates (e.g., crayfishes) throughout their life cycle (Hewson 1955; Paragamian 2009; Gardunio et al. 2011; McBaine et al. *in press*). In addition, Burbot are also highly fecund and exhibit aggregate spawning behavior (McPhail and Paragamian 2000). The majority of Burbot populations throughout their distribution are stable; however, populations along the northern tier of the United States are experiencing decline (Stapanian et al. 2000). This decline is especially apparent in populations like those in the Kootenai River, Idaho, and throughout Wyoming (Ireland and Perry 2008; Krueger and Hubert 1997; Hubert et al. 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

to the Green River basin in 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; Smith et al. 2016; Klein et al. 2016). Burbot pose a threat to ecologically important native fishes (i. e., Bluehead Sucker *Catostomous discobolus*, Flannelmouth Sucker *C. latipinnis*, Roundtail Chub *Gila robusta*, Colorado River Cutthroat Trout *Oncorhynchus clarki pleuriticus*), as well as economically important sport fishes (e.g., Brown Trout *Salmo trutta*, Rainbow Trout *Oncorhynchus mykiss,* Smallmouth Bass *Micropterus dolomieu,* kokanee *O. nerka*) through direct predation and competitive interactions (Klobucar et al. 2016; McBaine et al. *in press*). 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.

Suppression programs, though often effort-intensive and expensive, are feasible when supported by an in-depth understanding of the target species' life history and ecology (Chornesky and Randall 2003; Simberloff 2003; Mueller 2005). For example, 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 (Healey 1978; Hansen et al. 2008; Syslo et al. 2011). Regardless of the species targeted for suppression, demographic rate data on that population are needed before a suppression program is initiated.

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 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) and the population characteristics of Burbot in the reservoirs have not been described previously. Additionally, data from Burbot in reservoirs were unavailable and, therefore, not included in previous modeling efforts. Given that dynamic rates likely differ between lotic and lentic populations of Burbot (e.g., Fischer 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 from Burbot occupying lentic habitats in the Green River system are needed for comparison with estimates from Burbot in lotic habitats.

The objectives of our study were to describe the population characteristics of Burbot in Fontenelle and Flaming Gorge reservoirs to provide benchmarks for future monitoring programs. We also estimated the appropriate exploitation goals to suppress the Burbot population in lentic portions of the Green River. 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 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 and leaving the state at the Wyoming-Utah border. Flaming Gorge Reservoir is primarily located in Sweetwater County, Wyoming, with the southernmost portion of the reservoir located in Daggett County, Utah. As such, Flaming Gorge Reservoir fishery is managed by both the WGFD and the Utah Division of Wildlife Resources. 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 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 Brown Trout *Salmo trutta*, kokanee, Lake Trout, Smallmouth Bass, Rainbow Trout O. *mykiss,* White Sucker *Catostomus commersonii,* and Burbot (WGFD 2017).

Burbot were collected from Fontenelle Reservoir and Flaming Gorge reservoirs in October and November, 2016, using trammel nets. All nets were deployed in 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 hours. 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 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 total length (mm) and weight (g). Sex and maturity status was 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 ten Burbot per 10 mm length group and 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 stored in 5% formalin solution prior to fecundity estimation. Ovaries were only collected from fish 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 enumerated by one reader that possessed

previous experience ageing 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 section 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 of 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.

Analysis was conducted using the fisheries stock assessment (FSA) package in R (Ogle 2016; R Core Development Team 2016). Length structure was summarized using proportional size distribution (PSD; Gabelhouse 1984; Fisher et al. 1996; Neumann et al. 2012). Growth was evaluated using a von Bertalanffy growth model (Quist et al. 2012; Ogle et al. 2017). A nonlinear function was fit to back-calculated length-at-age data of subsampled Burbot using the following equation:

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

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 using the Dahl-Lea method (Campana 1990; Shoup and Michaletz 2017).

Instantaneous rate of mortality (Z) of 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 and Laude 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). Since an empirical estimate of instantaneous natural mortality (M) was unavailable, M was calculated using the Hoenig (1983) equation. Age-specific estimates of M were converted to annual survival rate (S) using the relationship $S = e^{-M}$ (Ricker 1975; Miranda and Bettoli 2007).

A female-based Leslie matrix was employed to estimate population growth rate of Burbot in the reservoirs impounding the Green River (Caswell 2000; Morris and Doak 2002). Demographic rates were similar 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 $Fert_1 - Fert_{12}$ are fertility rates for age-0 through age-12 Burbot and $S_1 - S_{11}$ 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 (0.5), 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 standard error (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 $0 - 1.5$ 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 Burbot sampling efficiency for various 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. 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 using the

"popbio" R package (Stubben and Milligan 2007; R Core Development Team 2014).

Population growth rate (λ_t) was calculated each year over 10, 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

A total of 923 Burbot was collected from Fontenelle ($n = 506$) and Flaming Gorge

reservoirs ($n = 417$). Burbot were large and varied in length from 218 mm to 985 mm with a

mean length of 534 mm (Figure 2). Proportional size distribution for Burbot in Fontenelle

Reservoir was 90 and 79 in Flaming Gorge Reservoir. Incremental PSD values were all higher

in Fontenelle Reservoir.

Ages of Burbot in our sample varied from 1 to 12 years (Figure 2). Total annual

mortality of Burbot in reservoirs was approximately 33% and estimated natural mortality was

29%. Given these estimates, angler exploitation was approximately 4%. The von Bertalanffy

growth model indicated that Burbot grow rapidly and can 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 length of 596 mm (Table 1). Fecundity for

female Burbot increased with age (Figure 4). Mean fecundity for age-3 Burbot was 183,799

(±SE; ±36,612) eggs and age-10 Burbot had a mean fecundity of 1,305,823 (±60,444) eggs

(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 $F \geq 0.15$. This corresponds 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

$F \geq 0.25$ ($\mu \geq 14\%$). In the final scenario where age-3 and older Burbot were fully selected, the

population would experience recruitment overfishing when $F \geq 0.49$ ($\mu \geq 33\%$). Population

growth rate 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 minimal. For example, a 10% reduction in survival of age-1 Burbot resulted in a 4% reduction in λ_G and a 10% reduction in survival of age-2 Burbot only resulted in a 3% reduction in λ_G over 10 years.

Discussion

Burbot are a top predator and have 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. *in press*). Klobucar et al. (2016) evaluated the trophic interactions of Burbot in Flaming Gorge Reservoir and found that Burbot have a relatively high level of diet overlap with Rainbow Trout (18 – 22%) and Smallmouth Bass (44%). In addition to potential competitive interactions, the authors suggested that Burbot could consume nearly double the biomass of Rainbow Trout annually stocked into the Flaming Gorge Reservoir (> 1 million individuals). Similarly, McBaine et al. (*in press*) found that fish composed an average of 75% of Burbot 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 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 its lotic counterpart.

Estimates of Burbot mortality in our study were low in comparison to Burbot sampled from the Green River and Burbot populations in their native distribution. Burbot in our study had a total annual mortality 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 ($A = 43\%$) than Burbot in our study. Due to low levels of exploitation in lotic environments of the Green River, the estimate of total annual mortality was also assumed to be the natural mortality level. Estimates of A in the lentic portions of the Green River were also lower than in other lentic populations throughout the species' distribution. For example, annual mortalities varying from 43 - 63% have been reported for Burbot across various Wisconsin lakes, and from 54 - 64% in the lakes and reservoirs of the Wind River basin, Wyoming (Schram 2000; Hubert at al. 2008). The low estimates of mortality from our study are likely due to the relative lack of fishing effort present in this system. Though no empirical estimate of angler exploitation exists for Burbot in the Green River, our estimate of exploitation is low (4%) compared to other river systems in Wyoming (Krueger and Hubert 1997). Reward-tag-return data collected at angling tournaments held on the study reservoirs suggests that our 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 of exploitation, 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 when compared to Burbot in the lotic portions of the system. Specifically, age-3 and age-6 Burbot in the Green River had mean lengths of 319 mm and 521 mm, whereas Burbot in the lentic portions of the Green River were 434 mm and 601 mm at the same ages. Growth in lentic portions of the Green River was comparable to growth of fish 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 mean maximum length (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 when compared 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 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). Burbot started to mature at age 2 and all age-5 Burbot were mature in Lake Superior (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 with fecundities often exceeding 1 million eggs per individual (Lawler 1963; Bailey 1972; Roach and Evenson 1993). Bailey

(1972) found that average fecundity of Burbot in Lake Superior was 812,300 eggs per female. Similarly, Lawler (1962) found that fecundities varied from 74,800 to 1,362,000 eggs and averaged 500,000 eggs per female in Heming Lake, Manitoba. Fecundity of Burbot in our study reservoirs was comparable to Burbot in the Green River and to populations of Burbot throughout their distribution. Fecundities of Burbot in the Green River were comparable and varied from 53,000 (250 mm) to 2,099,000 (682 mm) with an average of 621,000 eggs per individual (Klein et al. 2016). Our study found that fecundities of Burbot varied from 71,000 (368 mm) to 1,666,000 (852 mm) eggs and averaged 560,000 eggs per individual.

An age-structured population model indicated that population growth of Burbot in the study reservoirs was faster than for lotic populations. Early maturity, fast growth, and low mortality of reservoir-dwelling Burbot suggested that lentic populations of Burbot will continue to grow without some form of intervention. Our model suggested that Burbot populations in the study reservoirs increased 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 is 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 where Burbot were reared in earthen ponds and subjected to predation (Paragamian and Laude 2011). However, a lack of refuge habitat available to Burbot in the Paragamian and Laude (2011) study may have left juvenile Burbot overly exposed to predation. Despite this shortcoming, this estimate was also used to model age-0 Burbot survival by Klein et al. (2016), 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, our estimate of population growth rate is an underestimate. We also assumed that Burbot in the reservoirs of the Green River spawned annually. Burbot have been observed to skip spawning with spawning frequencies of 60 – 95% (Evenson 1990; Pullianen and Korhonen 1993). In Burbot populations with low juvenile survival, spawning frequency has been identified as a major driver in the viability of the population (Paragamian et al. 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 movement dynamics of Burbot. Preliminary results of a separate study evaluating movement suggests that a portion of the Green River Burbot population exhibits an adfluvial life history (Brauer et al. *In prep*). 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, our model results may be an overestimate of population growth. Additionally, model estimates from Klein et al. (2016) may be an underestimate if the spawning activity of adfluvial fish was not accounted for while modeling 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 information). 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 is implicated for 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 ~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 catch rates of Burbot using 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 where age-3 and older Burbot were selected for removal is likely the most realistic scenario for our study system. Under this scenario, exploitation would need to exceed 33% ($A \geq 57\%$) annually 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 exploitation 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 gill netting, trap netting, and angling has resulted in nonnative Lake Trout exploitation rates 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 other lentic populations of Burbot throughout their 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. Burbot populations in reservoirs of the Green River are growing rapidly and control of Burbot in the Green River system will likely be an arduous process. Exploitation will need to reach high levels and 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.

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Table 3.1. Mean vital rates and standard errors (SE) estimated from Burbot sampled from Fontenelle and Flaming Gorge reservoirs, Wyoming during the autumn and winter (2016-2017). Vital rate estimates and SEs were used to construct population matrices and model population growth.

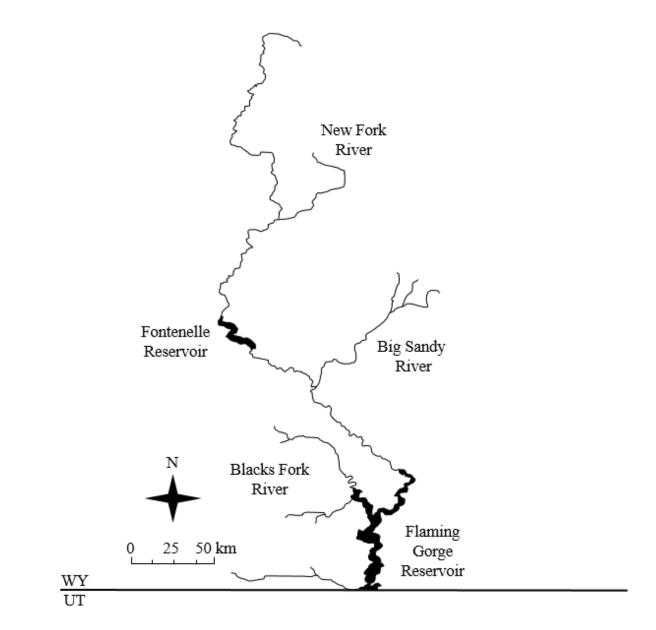| Symbol	Description	Age	Estimate	SE
f_t	Total fecundity	2	23,510	46,384
		3	183,799	36,612
		4	344,088	28,544
		5	504,377	23,968
		6	664,666	24,890
		7	824,955	30,821
		8	985,244	39,570
		9	1,145,534	49,668
		10	1,305,823	60,444
		11	1,466,112	71,592
		12	1,626,400	104,627
m_t	Probability of maturity (females)	2	0.330	0.086
		3	0.790	0.049
		4	0.820	0.032
		5	0.960	0.027
		6	1	-
		7	1	-
		8	1	-
		9	1	-
		10	1	-
		11	1	-
		12	1	-
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

Figure 3.1. Map of the Green River basin including its major tributaries and associated reservoirs. Burbot were sampled from Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, during autumn and winter (2016 - 2017).
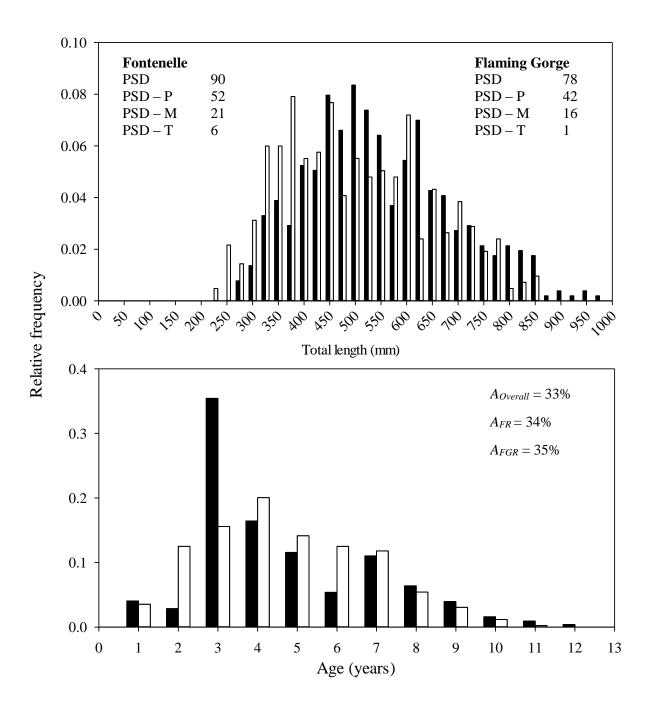
Figure 3.2. Length and age distributions of Burbot sampled in Fontenelle (FR; black bars) and Flaming Gorge (FGR; white bars) reservoirs, Wyoming in autumn and winter (2016-2017). Proportional size-distributions are provided for stock (PSD), preferred (PSD-P), memorable (PSD-M), and trophy (PSD-T) size classifications. Total annual mortality (*A*) estimates are also provided.
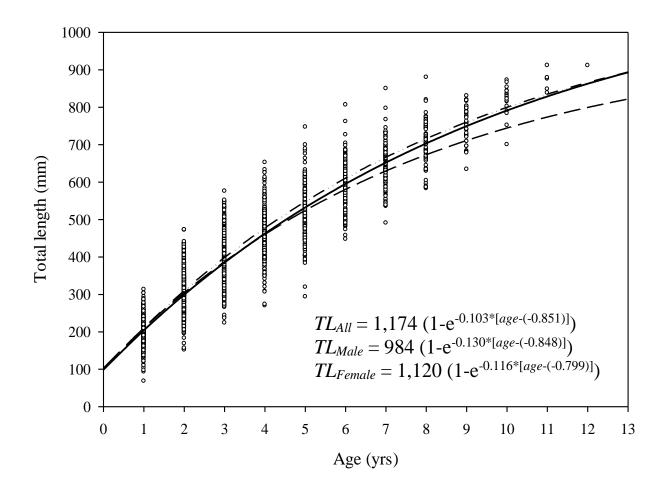
Figure 3.3. Back-calculated length-at-age and von Bertalanffy growth model for female Burbot (dot-dashed line), male Burbot (dashed line), and both sexes combined (solid line). Fish were sampled in Fontenelle and Flaming Gorge reservoirs, Wyoming during autumn and winter (2016-2017).
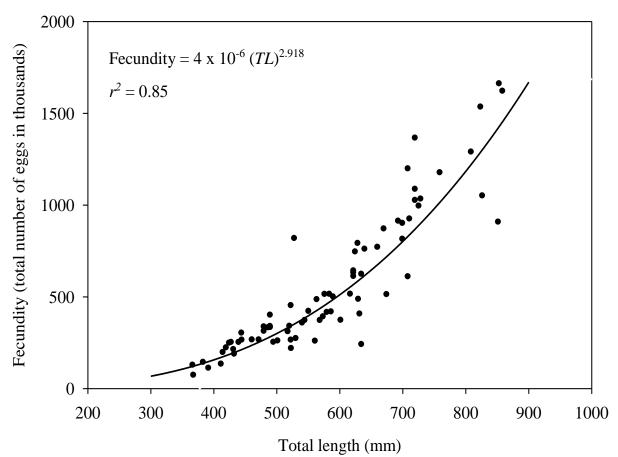
Figure 3.4. Fecundity-length relationship for Burbot sampled in Fontenelle and Flaming Gorge reservoirs, Wyoming during autumn (2016). The solid line and equation represents the fitted regression model. The r^2-value is provided as an estimate of model fit.
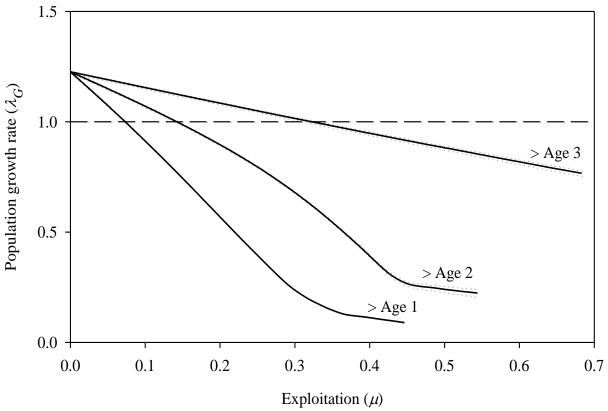
Figure 3.5. Population growth rate (λ_G) over a 10-year time period for Burbot sampled from Fontenelle and Flaming Gorge reservoirs during the autumn and winter (2016-2017). Population growth was calculated assuming fishing pressure fully selected for age-1 and older Burbot, age-2 and older Burbot, and age-3 and older Burbot. Dotted lines represent 95% confidence intervals for estimates of λ_G. The horizontal dashed line represents $\lambda_G = 1$ (replacement).
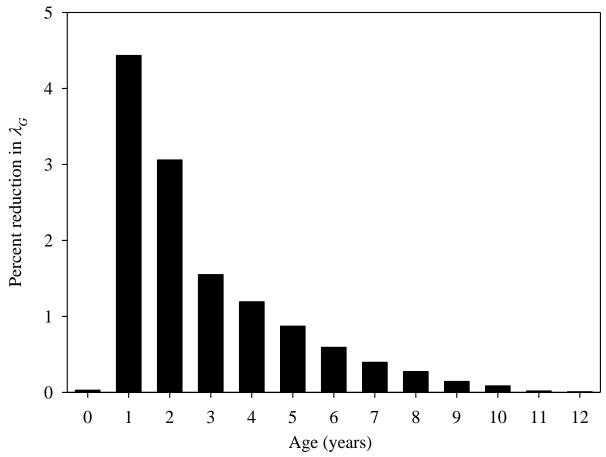
Figure 3.6. Percent reduction in population growth rate (λ_G) given 10% reductions in age-specific survival of Burbot in Fontenelle and Flaming Gorge reservoirs, Wyoming sampled during autumn and winter (2016-2017).

Chapter 4. Movement Dynamics of Nonnative Burbot in the Upper Green River System and Implications for Management

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Abstract

Burbot *Lota lota* were illegally introduced to the Green River, Wyoming, in the mid-1990s and pose a threat to recreational fisheries and native fish conservation. Although much is known about Burbot population dynamics, little is known about their movement patterns in the Green River system. Our objectives were to describe the movement dynamics of Burbot in the upper Green River system to provide information on the ecology of Burbot and insight on possible management actions. In total, 875 Burbot were tagged with passive integrated transponder (PIT) tags in the upper Green River within 57 km of Fontenelle Reservoir and throughout Fontenelle Reservoir. Movements of tagged fish between reservoir and river habitats were tracked using a stationary PIT antenna located near the mouth of the upper Green River from August 2016 - March 2018. Additionally, 22 Burbot were tagged with radio-transmitters in Fontenelle Reservoir in November 2017. Of these fish, 11 Burbot were tracked as they migrated into the Green River and associated tributaries during the spawning season. Upstream and downstream movements of Burbot tagged with PIT tags in Fontenelle Reservoir and the upper Green River peaked during December - January and were synchronized with river temperatures reaching 0°C. Of the total number of Burbot PIT tagged, 13% tagged in Fontenelle Reservoir were detected in the Green River during the spawning season and 19% of Burbot tagged in the Green River were detected moving downstream towards Fontenelle Reservoir during the spawning period. Movements of radio-

telemetered Burbot were synchronized with river ice-up in mid-December. Maximum

upstream distance travelled by adfluvial Burbot was 5.8 km and the majority of fish migrated

less than 3 km upstream before returning to the reservoir. Relocation data suggest that Burbot

do not move long distances and areas within 3 km of Fontenelle Reservoir are important for

spawning. Results of this study assist with the management of Burbot in this system by

identifying areas and timing of high Burbot use that can be targeted for suppression programs.

Results also contribute to our understanding of variability in Burbot ecology beyond their

native distribution.

Introduction

Freshwater fishes exhibit a diversity of movement behaviors and life history strategies

(Mann et al. 1984). These life history strategies are often of interest to fishery managers due

to the influences that individual movement behaviors may have on population status (Pine et

al. 2012). Freshwater fish generally employ one of four life history strategies including

resident (i.e., river dwelling and spawning), fluvial (i.e., river dwelling, tributary spawning),

adfluvial (i.e., lake dwelling, river or stream spawning), and anadromous variants (i.e., ocean

dwelling, river spawning). A fish population can have multiple life history variants occurring

simultaneously. Each life history variant group in a population can be affected by different

factors and managers must understand the population's structure to ensure effective

management (Jonsson 1985; Trotter 1989; McPhail and Baxter 1996; Peterson et al. 2007).

Inability to assess behavioral and life history differences in fish populations can result in the

overexploitation (Ying et al. 2011) and (or) the misallocation of resources (e.g., rehabilitation

of unimportant habitats; Binns 2004; Pegg and Chick 2010). For example, adfluvial Bull

Trout *Salvelinus confluentus* in Lower Kanaskis Lake, Alberta, were subject to high

exploitation rates during their spawning season as they became more vulnerable to angling in

the shallow tributaries compared to the deep-water habitat they used during the non-spawning

season. By closing the fishery in tributary streams, the population experienced a 28-fold

increase in abundance over a 10-year period (Johnston et al. 2007). Similarly, a review by

Cunjak (1995) suggested that increases in salmonid production brought on by summer habitat

improvement projects were frequently nullified by a rivers overwinter habitat carrying

capacity and subsequent movements of fish out of rehabilitated reaches.

      In addition to managing socially important fishes, assessments of population structure

and movement dynamics are also crucial when designing removal programs that target

undesirable species, especially when that species is known to exhibit multiple life history

strategies. Understanding movement dynamics and population structure of undesirable species

can often make removal efforts more effective. For example, Lake Trout *Salvelinus*

namaycush inhabit deep lakes throughout a majority of the year and are less susceptible to

most sampling gears; however, they often congregate in shallow waters to spawn and are

vulnerable to removal efforts at that time (Gunn 1995). Numerous nonnative Lake Trout

populations throughout the western United States have been targeted for removal by focusing

suppression efforts on spawning congregations (Syslo et al. 2011). Similar methods have been

used to suppress Common Carp *Cyprinus carpio* in the midwestern United States. Bajer et al.

(2011) achieved 52-94% removal from four midwestern reservoirs by targeting winter-time

aggregations of Common Carp using commercial seines. Effective suppression programs such

as these provide a model for fishery managers that are addressing the effects of nonnative

species in their own jurisdictions. The situation surrounding nonnative Burbot in the Green

River basin (GRB), Wyoming, is one such example where an understanding of movement dynamics and populations structure is critical for developing effective management strategies.

Burbot are native to northern Wyoming in the Wind-Big Horn and Tongue river basins (Baxter and Stone 1995). Like many native populations of Burbot in the United States, Burbot populations in Wyoming have declined. They have been extirpated from the Tongue River system and occur at low densities in the Wind-Big Horn River drainage which has prompted their designation as a "species of greatest conservation need" in Wyoming (Krueger and Hubert 1997; Hubert et al 2008; Underwood et al. 2016; WGFD 2017). In these systems, management is focused on conservation and protection of native Burbot populations. Burbot are also present in the GRB due to unauthorized introductions in the 1990s where they illicit a very different management response given their invasive nature (Gardunio et al. 2011). Given the potential of Burbot to negatively affect socially and ecologically important fishes in the Green River system through predation and competitive interactions (i.e., Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *Catostomus discobolus*, and Roundtail Chub *Gila robusta*), the Wyoming Game and Fish Department (WGFD) has expressed interest in a suppression program to target Burbot throughout the Green River system (Klein et al. 2015a; 2015b; 2016; Klobucar et al. 2016; Brauer at al. 2018; McBaine et al. 2018). However, before a suppression effort can be implemented, an in-depth understanding of the movement dynamics and population structure of Burbot must be attained to effectively allocate suppression efforts.

Burbot is a holarctically distributed top predator that occurs throughout a diversity of lotic and lentic habitats (McPhail and Paragamian 2000). Similar to gadiforms in marine environments (e.g., Atlantic Cod *Gadus morhua),* Burbot have exhibited both resident and

migratory behavior (Cote et al. 2004). In some lotic systems, fluvial Burbot migrate long

distances to spawning sites, sometimes travelling over 100 km (Evenson 1993). Some

lacustrine populations of Burbot have demonstrated an adfluvial life history where they

occupy a lake and use tributary streams for spawning (Paragamian 2000; Schram 2000).

Burbot spawn in aggregate during the winter season (McPhail and Paragamian 2000) and

these aggregations represent a potential target for suppression efforts as targeting these sites

will likely increase the efficiency of removal efforts. However, the locations of spawning

areas and the timing of fish movements to these areas in the GRB are unknown. Since 2001,

Burbot have been consistently sampled in both the Green River and its associated reservoirs

(i.e., Fontenelle Reservoir, Flaming Gorge Reservoir; Gardunio et al. 2011; Klein et al. 2016).

Anecdotal evidence suggests that proportions of Burbot in the upper Green River system

exhibit both adfluvial and resident movement behaviors (Klein et al. 2015b). Movements of

Burbot between reservoir and river environments may influence the effectiveness of removal

efforts by informing previously developed population models that did not account for

movement. Movement may influence Burbot population dynamics in the GRB due to the

addition and(or) subtraction of individuals from reservoir and river environments. If Burbot

in the upper Green River system exhibit migratory behavior, understanding the timing of

movements, as well as the location of high-use areas of river (i.e., spawning locations), will

aid in the management of Burbot populations in the system. The objective of this study was to

describe the timing and patterns of Burbot movement in the upper Green River system.

Additionally, we sought to identify areas of high use by Burbot that may serve as targets for

suppression efforts. Overall, this study meant to provide data to aid in management and

provide information on the ecology of nonnative Burbot.

Methods

Study area

The Green River is the largest tributary to the Colorado River, draining portions of Colorado, Utah, and Wyoming. This study took place in the upper portion of the Green River system from Fontenelle Dam to the headwater region of the Green River. The upper Green River originates in the Wind River Range of western Wyoming and flows approximately 235 km before entering Fontenelle Reservoir (Figure 1). Fontenelle Reservoir is an artificial impoundment primarily used for flood control with a secondary use of hydroelectric power generation. At capacity, the reservoir has a surface area of approximately 3,200 ha and a maximum depth of about 30 m. Upstream of Fontenelle Reservoir, the Green River is characterized by high-gradient runs interspersed with pool-riffle habitat and substrate dominated by alluvial deposits (i.e., cobble, gravel, sand, and silt; Kurtz 1980). Most of the GRB is typical of a high desert climate with monthly average temperatures of -9°C (January) and 17°C (July), and low annual precipitation (25.4 cm; WGFD 2017). During the winter season, the majority of the upper Green River and Fontenelle Reservoir is covered with ice. Ice-up generally occurs in late-November to early-December and ice-out typically occurs in March along with low-elevation runoff.

Data collection

A dual application of passive integrated transponder (PIT) and radio-telemetry technology was used to describe Burbot movements in this system. Passive integrated transponder tags were intended to describe coarse-scale movement patterns of Burbot tagged

in the Green River and Fontenelle Reservoir. Radio telemetry was used to describe fine-scale movement patterns of adfluvial Burbot in Fontenelle Reservoir. We were primarily interested in identifying areas of high Burbot use and the extent and timing of migrations undertaken by adfluvial Burbot.

Passive integrated transponder (PIT) evaluation

In July 2016, two identical flat-panel half-duplex (HDX) passive integrated transponder antennae were installed in the Green River 7 km upstream of Fontenelle Reservoir (Figure 1) and was active from July – March, 2016 – 2018. The site was chosen due to its proximity to Fontenelle Reservoir, comparatively narrow channel, accessibility, and cooperation by landowners. Each antenna covered one half the river channel (~50 m each). Antennae were a pass-over design that minimized potential damage from high-velocities. Antenna efficiency was measured using a large-scale detection test modified from Compton et al. (2008). Briefly, a PIT tag was passed over the antenna at 1 m intervals at substrate, mid-column, and surface depths. The tag was held parallel and perpendicular to the antenna at each location. Combined detection efficiency for the array was 86% under base flow conditions and effective read range was approximately 30 cm. The system did not differentiate between upstream and downstream movements. Initial movement direction was inferred by release location of tagged fish. Movement direction of individual Burbot following the initial detection was estimated based on the direction of the previous movement direction. Antennae recorded movements of Burbot for the project duration except for periods of high flow (spring-summer season) when they were removed to avoid damage to PIT electronics.

Burbot were tagged with PIT tags in the upper Green River in the summer of 2016 and 2017, and in Fontenelle Reservoir during the fall of 2016 and 2017. Fish in the upper Green River were collected using drift-boat-mounted electrofishing gear in the section of river beginning at the PIT antenna array to a point 50 km upstream of the array. Power output was standardized to 2,750-3,250 W (Miranda 2009) and sampling took place after sunset to maximize catch rates (Witt and Campbell 1959; Paragamian 1989; Klein et al. 2015a). Fish in Fontenelle Reservoir were collected using trammel nets. Trammel nets were 48.8 m long and 1.8 m tall and consisted of 25.4-cm bar outer mesh and 2.5-cm bar inner mesh. Nets were set perpendicular to shore at varying depths (<20 m) and anchored at both ends. Net locations were placed in standardized locations used by WGFD during annual Burbot surveys, or near those locations when additional netting effort was required.

All captured Burbot were enumerated, measured for total length (mm) and weight (g), and implanted with a 23-mm half-duplex PIT tag (Oregon RFID, Portland, Oregon). Tags were injected into the peritoneal cavity just off the midline, posterior to the pectoral fin using a syringe applicator due to the high retention rate (>95%; Ashton et al. 2014). The tag identification number was recorded to identify individual fish. A sample of fish tagged in Fontenelle Reservoir ($n = 50$) were placed in a net pen submerged to a depth of 10 m to evaluate short-term mortality due to tagging and handling. After a period of 24 hours, the net pen was brought to the surface so mortality and tag retention could be evaluated. Short-term survival was 98% and short-term tag retention was 100%. We were unable to evaluate short-term mortality and tag retention for fish tagged in the Green River due to the logistics of holding fish for a long period of time. Tagged fish were released as close as possible to

capture locations and all release locations were georeferenced using a global positioning system (GPS) unit.

Radio telemetry

We sought to identify the movement dynamics of adfluvial fish; therefore, we allocated radio tags to Burbot in Fontenelle Reservoir. Burbot in Fontenelle Reservoir were collected using trammel nets in late-November 2017. Adfluvial Burbot are known to stage near river mouths prior to migrating upstream for spawning (McPhail and Paragamian 2000). For that reason, trammel netting focused on the upstream portion of the reservoir to improve the probability that a tagged fish was adfluvial. Only large Burbot (>550 mm) were chosen for radio-transmitter implantation to increase the probability that tagged Burbot were mature (Klein et al. 2016). Additionally, Burbot in the upper Green River were collected for radio transmitter implantation in August 2017. Riverine Burbot were collected by methods like those used to collect fish for PIT tag implantation.

Burbot selected for transmitter implantation were anesthetized using MS-222 (100 mg/L, Agent Chemical Laboratories, Inc., Washington) before total length (mm) and weight (g) were recorded. Fish were placed in a supine position and individually-coded MCFT2-3EM radio transmitters (Lotek Wireless, Newmarket, Ontario) were implanted into a 1-2 cm incision in the peritoneal cavity (Jakober et al. 1998). Transmitters were programmed to 150.570 MHz with a 5.0 s burst interval. Minimum battery life for transmitters was 250 days. Antennae exited the body wall using a shielded-needle technique (Ross and Kleiner 1982). Incisions were closed with 2-3 interrupted sutures. Tag weight (10 g) was less than 3% of total fish weight (Zale et al. 2005), and surgeries were kept under 10 min in duration to

minimize stress on the fish. Prior to release, fish were allowed to recover in aerated live wells until they regained equilibrium and responded to touch stimulus (>20 minutes). Fish were released as close as possible to their original capture location.

Radio-tagged Burbot were tracked on foot and using fixed-wing aircraft from October 2017 to February 28th, 2018. Based on PIT tag movement data from 2016, this period likely coincided with the Burbot spawning season. Mobile tracking equipment consisted of a portable three-element Yagi antenna in conjunction with a SRX 800 receiver modified for portability (Lotek Wireless, Newmarket, Ontario). Antennae error was measured using similar methods to those described by Simpkins and Hubert (1998). Tags were placed underwater and tracked by an observer possessing no knowledge of tag location at various distances from the tag. Error was measured as the distance between a tag's true location and its estimated location. Location error was 1.1 m (SE = 0.2 m) at 10 m to the radio transmitter and decreased to 0.6 m (± 0.1 m) at 5.0 m. Foot-based tracking was conducted multiple times weekly and commenced at the uppermost section of the study area in a downstream direction. Foot-based tracking was conducted in the section of river within 57 km of the mouth of the upper Green River. Aircraft-based methods tracked fish throughout Fontenelle Reservoir and the entire upper Green River on a monthly basis. Aircraft-based telemetry accuracy was assessed by comparison with known-location radio-transmitters. Aircraft relocations were less accurate than foot-based relocations and error averaged 68 m (± 43 m). Once a fish was relocated, its location in the river channel was recorded and georeferenced using a GPS unit. Temperature data for the Green River were collected using a U.S. Geological Survey monitoring station located 200 m upstream of the PIT antennae array.

Data analysis

  The initial release locations of fish tagged with PIT tags were uploaded into ArcMap V. 10 (Environmental Systems Research Institute, Redlands, California) for analysis. Fish movement was expressed as the total distance between initial release location and each relocation at the PIT antenna (Muhlfeld and Marotz 2011; Dobos et al. 2016). Distances and timing of movements were summarized by tagging location (i.e., river or reservoir). Movement of Burbot tagged with radio transmitters was summarized based on the extent of movement and daily movement rate. Extent of movement was defined as the difference between the initial release location and the farthest upstream or downstream relocation of a fish throughout the study period (Langhurst and Schoenike 1990). Daily movement rate was calculated as the total distance moved divided by the number of days between subsequent relocations (Dobos et al. 2016). Upstream movement was expressed as a positive value and downstream movements were expressed as negative values. Movements were summarized for Burbot during the spawning period. Pre-spawn and spawning periods were defined based on observed movement patterns in the study system and considered to occur during the period between river ice-up to the onset of low-elevation runoff (December-March). We estimated that a fish had returned to its pre-spawn location once an adfluvial fish had moved from the river to the reservoir.

  A kernel density estimator was used to examine the proportional use of the upper Green River by radio-tagged Burbot during the spawning season (Vokoun 2003). Histograms of relocations along the upper Green River were used to obtain the density estimate. Areas with a high probability of use by Burbot were illustrated by peaks in the utilization

distribution and indicate potential spawning locations of adfluvial Burbot. The univariate

kernel density estimator was defined as

$$\hat{f}(x) = \frac{1}{nh} \sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right)$$

where h was the bandwidth and $K(x)$ was the Gaussian kernel function (Vokoun 2003;

Vokoun and Rabeni 2005). The appropriate bandwidth was selected using a Sheather-Jones

plug-in method (Jones et al. 1996). Kernel estimates were calculated for the entirety of the

Burbot spawning season in 2017.

Results

Eight hundred and seventy five Burbot were implanted with PIT tags. Of these, 421

were tagged in the Green River ($n_{2016} = 280$, $n_{2017} = 141$) and 454 were tagged in Fontenelle

Reservoir ($n_{2016} = 237$, $n_{2017} = 217$). Fish tagged in the Green River varied in length from 200

to 633 mm (mean $\pm$ SD; 377 ± 90 mm) and fish tagged in Fontenelle Reservoir varied in

length from 282 to 985 mm (535 ± 146 mm; Figure 2). Of the fish tagged in the upper Green

River, 81 (19%) were detected moving downstream toward Fontenelle Reservoir during the

spawning period ($n_{2016} = 37$, $n_{2017} = 44$). Relocated river-tagged fish varied in length from 230

to 618 mm (382 ± 71 mm; Figure 2). In total, 59 (13%) of the Burbot tagged in Fontenelle

Reservoir were relocated at the PIT antenna ($n_{2016} = 37$, $n_{2017} = 22$). Relocated reservoir-

tagged Burbot varied in length from 414 to 850 mm (617 ± 114 mm). Lengths of reservoir-

tagged Burbot relocated in the Green River were skewed toward larger length classes

compared to the length distribution of all tagged fish.

Movements of Burbot PIT tagged in the Green River corresponded with water

temperatures reaching 0°C (Figure 3). Initial relocations of river-tagged fish began in late

November and relocations peaked in early to mid-December. Of the relocated river-tagged fish, 54% were subsequently relocated. We made the assumption that these fish were moving back upstream. Mean time spent downstream of the antenna was 30 days (SE = 21 d). Relocations of Burbot tagged in Fontenelle Reservoir moving upstream were highly synchronized. Relocations primarily occurred during the last two weeks of December in both 2016 and 2017. Like Burbot tagged in the river, movements of fish tagged in the reservoir primarily occurred once water temperatures reached 0°C. Mean time spent upstream of the PIT antenna for reservoir-tagged Burbot was 21 days (SE = 14 d).

Approximately 31% of the Burbot tagged within 12 km upstream of the antenna were relocated moving downstream (Figure 4). Relocated fish that were tagged in this section of river accounted for 79% of the total number of initial relocations for river-tagged fish. Of the total initial relocations of river-tagged fish, 96% were released within 24 km of the PIT array. The maximum distance travelled downstream by a relocated PIT-tagged Burbot was 35 km.

In total, 40 radio transmitters were implanted in Burbot. Eighteen transmitters were implanted in Burbot from the upper Green River in August 2017 and 22 Burbot were implanted with radio transmitters in Fontenelle Reservoir in November 2017. Total length of radio-tagged fish in the Green River varied from 430-711 mm (mean ± SD; 509 ± 71 mm). Total length of radio-tagged fish in Fontenelle Reservoir varied from 560-905 mm (713 ± 100 mm). No relocations were made for river-tagged fish due to high tag-failure rates (>60%) and mortality. Of 22 tagged fish in Fontenelle Reservoir, 10 were relocated in the Green River and one was relocated in the mouth of Fontenelle Creek, a tributary to Fontenelle Reservoir. The remaining 11 fish were not relocated due to attenuation caused by the depth of the reservoir or transmitter malfunction. In total, 191 relocations were made on radio-tagged Burbot (Figure

5). Similar to movement of PIT-tagged fish, radio-tagged Burbot movement into the Green River was synchronized. All fish entered the Green River from December 10 - 16 after river temperature dropped to 0°C. Once in the Green River, movement patterns were variable among individual Burbot. Maximum upstream distance travelled by a fish from its release site in Fontenelle Reservoir was 13.2 km (Figure 5). However, maximum upstream distance travelled from the mouth of the river was only 5.8 km. Mean daily movement rates for Burbot varied from -30 to 142 m/day (67 ± 59 m/day). Upstream movements generally occurred over a short time period and fish remained sedentary upon reaching suspected spawning areas. Kernel density estimates suggested a high probability of Burbot use between river kilometers 19-21 during the spawning season (Figure 6). Habitat used by Burbot within 3 km of Fontenelle Reservoir was characterized by low-velocity runs and pools with coarse substrate and close proximity to alluvium-bluff banks. Habitats used by adfluvial Burbot upstream of 3 km were primarily low-velocity runs.

Discussion

Burbot movement dynamics have been studied throughout their distribution (Evenson 1993; Carl 1995; Arndt and Hutchinson 2000; Schram 2000; Paragamian et al. 2005; Dunnigan and Sinclair 2008; Dillen et al. 2008; Paragamian and Wakkinen 2008). Although patterns in movement vary based on their geographic location, prior research suggests that movement is generally highest during the pre-spawn and spawning period (i.e., winter). In the Tanana River, Alaska, Burbot movement was most prevalent during winter months and coincided with river ice-up (Evenson 1993). Similarly, movement of radio-tagged Burbot in the Kootenai River, Idaho, peaked during winter months when water temperatures dropped

below 4°C (Paragamian and Wakkinen 2008). Both PIT and radio-tagged Burbot in our study exhibited peak movement during the spawning season. In fact, movements were almost entirely observed after water temperatures reached 0°C, when both the upper Green River and Fontenelle Reservoir were covered in ice. The relationship between Burbot spawning movements and temperature was similar in our study to other systems, but the timing of movements and the suspected spawning period were dissimilar. Specifically, Cott et al. (2013) reported little variation in the timing of spawning in 24 lacustrine Burbot populations throughout Canada, regardless of differences in environmental conditions (e.g., duration of ice cover). Spawning generally occurred during the first three weeks of February in these populations. In our study, Burbot in the Green River likely spawn primarily in January. Movement data suggest that Burbot conducted pre-spawn movements synchronously in mid-December and returned to their pre-spawn locations after a period consistent with other populations reviewed in Cott et al. (2013). This dissimilarity in movement patterns may be the result of a much earlier onset of freezing water temperatures in the Green River basin. In addition, Burbot movements have not been previously described outside of their native distribution, so comparisons with other populations may be somewhat tenuous.

Adfluvial life histories are common in Burbot populations (Sorokin 1971) and given the lentic origin of Burbot illegally introduced in the Green River (Boysen Reservoir, Wyoming; Underwood et al. 2016), it is not surprising that they are exhibiting historic adfluvial life history traits in their adopted river system. Burbot have shown to exhibit high ecological plasticity which may explain their success in the Green River system. For example, hatchery-reared lake-origin Burbot adopted riverine environments over lacustrine environments when stocked into the Kootenai River, Idaho (Hardy et al. 2015). Our study

suggests that a portion of the Burbot population in Fontenelle Reservoir exhibits an adfluvial life history. Of the total fish PIT-tagged in Fontenelle Reservoir, 10-15% were detected in the upper Green River throughout the spawning season depending on the year of the study. Additionally, only mature fish seemed to be making migrations based on length distribution of relocated fish.

Relocations of radio-tagged Burbot suggested that adfluvial movements were over short distances. The distances travelled by adfluvial fish in our study were different from those of other adfluvial populations of Burbot. For example, Schram (2000) documented upstream migrations of Burbot over 50 km from Lake Superior, Wisconsin, into various tributaries. Fluvial Burbot also exhibit long migrations, sometimes exceeding 200 km (Evenson 1993). In our study, radio-tagged Burbot travelled a maximum of 6 km into the Green River with most fish staying within 3 km of Fontenelle Reservoir. Spawning habitats occupied by adfluvial Burbot in our study are consistent with habitats selected by Burbot during the summer and fall (Klein et al. 2015a). No radio-tagged Burbot moved as far upstream as our PIT antenna, highlighting the importance of the lower portion of the upper Green River to the Fontenelle Reservoir Burbot population. The fact that all radio-tagged Burbot stayed downstream of our PIT array may suggest that our estimate of the proportion of adfluvial Burbot (using PIT tags) in Fontenelle Reservoir is an underestimate. Our PIT tag data also suggest that fluvial Burbot travel downstream towards these sites and return upstream after the spawning period. Approximately 19% of Burbot PIT-tagged in the Green River demonstrated downstream movements during the spawning season. Most of these fish were caught and tagged within 20 km of the reservoir. While we have no direct evidence of spawning activity for these fish, other Burbot populations have exhibited extensive

downstream movements to reach spawning sites (Robins and Duebler 1955; Evenson 1993) and many Burbot in the Green River may be exhibiting similar, albeit shorter, movement patterns. However, without complimentary radio telemetry data for fluvial Burbot, assumptions made regarding the purpose of downstream movements may be tenuous. From a management perspective, short Burbot migration distances may benefit a suppression program because spawning is likely occurring in a relatively small section of the upper Green River. Targeting the area within 6 km of Fontenelle Reservoir may improve the overall efficiency of removal efforts. However, mechanical removal of Burbot during the spawning season may be difficult and dangerous since the Green River is covered in ice during that period. Despite the inherent difficulties brought on by ice cover, this section of the Green River could also be targeted during the spring months after the spawning season. Prior research suggests that increases in mortality of juvenile Burbot have the greatest effect on reducing Burbot population growth (Klein et al. 2016). Beard et al. (2017) observed low levels of dispersion for juvenile Burbot stocked in Deep Creek, Idaho. If wild juvenile Burbot exhibit similar movement patterns in the Green River, targeting these sites after ice-off may increase the efficiency of removal efforts on juvenile age-classes.

The objective of this study was to identify the movement dynamics Burbot in the upper GRB. Due to a mixture of high tag failure rates (over 60%) and suspected mortality, we were unable to track fish that were radio-tagged in the Green River. Of the five suspected mortalities, three tags were located above the high-water mark. Two of these tags were found near River Otter *Lontra canadensis* latrine sites and one tag was found at the base of a large tree containing an Osprey *Pandion haliaetus* nest. The remaining two unconfirmed mortalities were considered dead due to lack of movement over a 5-month period and because they were

in areas of river that were not favorable for Burbot (i.e., very shallow). The high tag failure rate observed in our study was the result of frequency drift caused defective tag crystals. The high mortality rate of radio-tagged Burbot in the Green River may be a result of the riverine fish being exposed to high water temperatures during tagging (13 – 15 °C). Tags that were located above the high-water mark may be the result of direct predation or scavenging of dead Burbot by terrestrial and avian predators. Given the difficulties we experienced regarding radio-tagged fish in the Green River, repeating this portion of the study by tracking river-tagged fish may be warranted. Additionally, identifying spawning areas in Fontenelle Reservoir will also provide managers with areas to target in both river and reservoir environments.

This study provides critical insight into the movement dynamics of Burbot in the upper Green River system. Given the potential of Burbot to alter the food web in the Green River, understanding their movement dynamics will both increase the effectiveness of suppression efforts and provide insight on potential interactions of Burbot with important native and sport fishes. The results of this research suggest that a substantial portion of the Burbot population in the upper Green River exhibits an adfluvial life history. Fish movements are generally short in distance with the majority of suspected spawning locations occurring in close proximity to Fontenelle Reservoir. Potential spawning locations described in this study also provide a target for suppression efforts. Additional insight into the movement dynamics of riverine Burbot in the Green River system will further assist with their management. This research also provides insight into the ecology of Burbot outside of Wyoming, and may assist in the management of imperiled Burbot populations throughout their distribution by further demonstrating the possible variability in Burbot ecology among populations.

Acknowledgements

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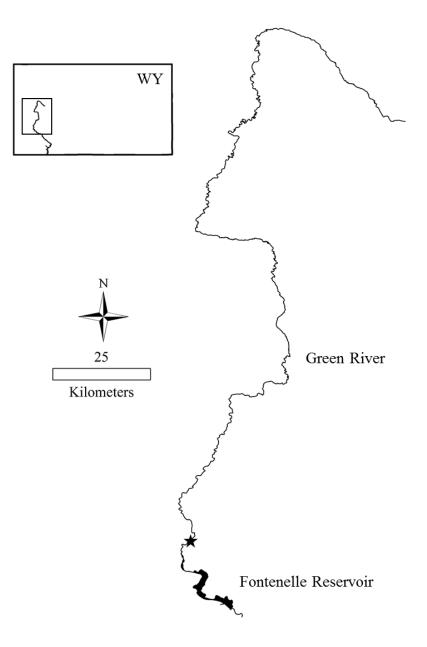
Figure 4.1. Map of the upper Green River and Fontenelle Reservoir. Burbot were sampled from the upper Green River and Fontenelle Reservoir, Wyoming, during summer and autumn (2016 - 2017). This study was conducted in the portion of the system from Fontenelle Reservoir upstream to the headwaters of the Green River. The location of a passive integrate transponder array is indicated by a star.
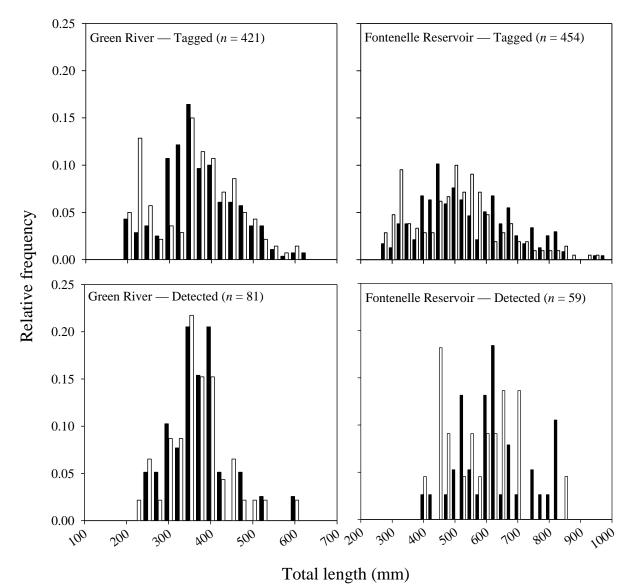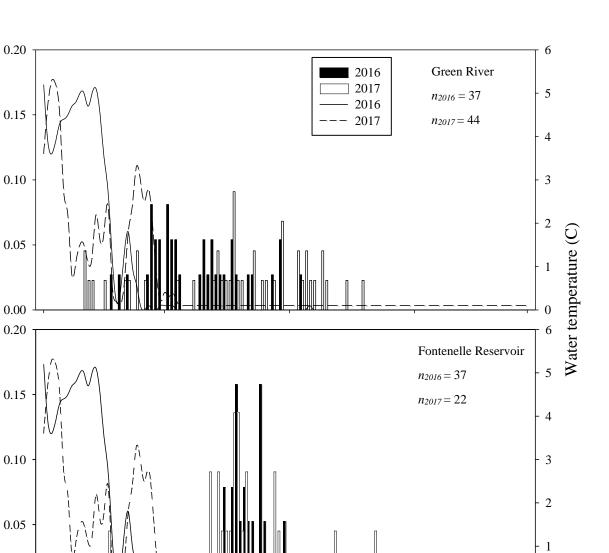
Figure 4.2. Length-frequency distributions of Burbot tagged in the upper Green River and Fontenelle Reservoir, Wyoming, and for Burbot detected at a passive integrate transponder antenna located near the mouth of the upper Green River in 2016 (black bars) and 2017(white bars).

Figure 4.3. Histograms depicting the timing of detections of Burbot passive integrated transponder (PIT)-tagged in Fontenelle Reservoir and the upper Green River, Wyoming at a stationary PIT antenna array located 7 km upstream of Fontenelle Reservoir. Frequency of detections and mean daily water temperature for the upper Green River in 2016 (black bars; solid line) and in 2017 (white bars; dashed line) are provided. Total number of individuals detected are provided for 2016 and 2017
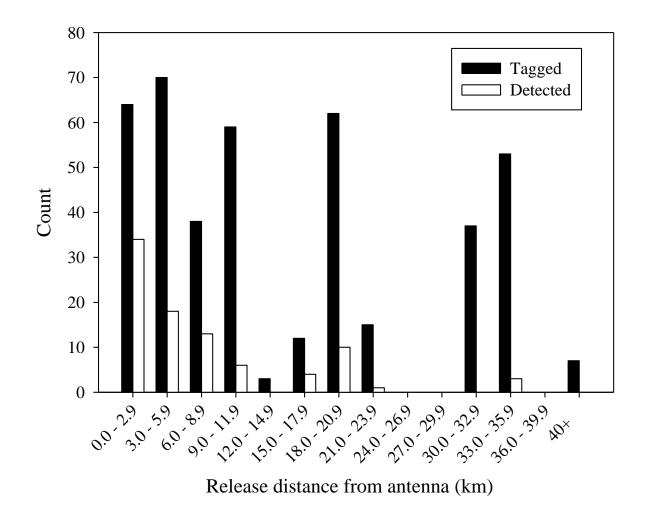
Figure 4.4. Histogram depicting total number of Burbot tagged with passive integrated transponder (PIT) tags in the upper Green River (black bars) and total number of Burbot redetected at the PIT antenna (white bars) in relation to the distance a fish was tagged and released (km) from the PIT antenna. Data from 2016 and 2017 are included.
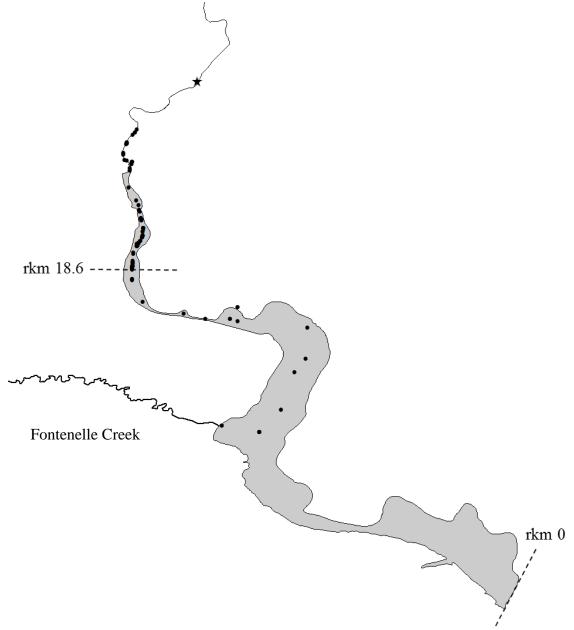
Figure 4.5. Redetection locations (black dots) for radio-telemetered Burbot in Fontenelle Reservoir and the upper Green River, Wyoming during winter 2017-2018. The dotted line represents the mouth of the upper Green River (river kilometer [rkm] 18.6) and Fontenelle Dam (rkm 0) from December 2017 – February 2018. The location of the passive integrated transponder array is indicated by a star.
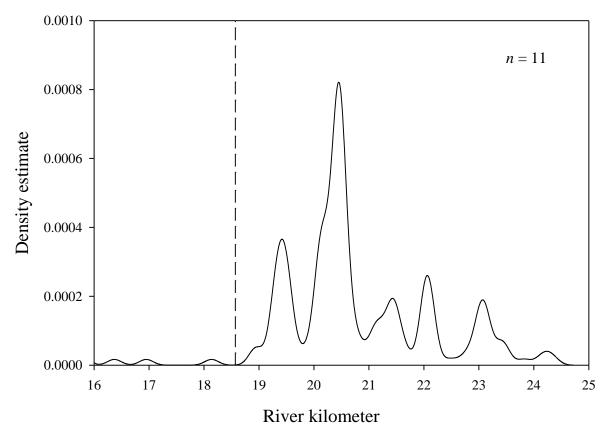
Figure 4.6. Kernel density estimates for winter detections of radio-tagged Burbot in the upper Green River, Wyoming in 2017-2018. The horizontal dashed line (river kilometer 18.6) represents the mouth of the upper Green River. The number of Burbot detected is included.

Chapter 5. General Conclusions

The goal of this thesis was to provide additional information on the ecology of Burbot outside their native distribution. The results presented in this thesis are meant to inform the management of nonnative, undesirable Burbot. Each chapter addresses an aspect of Burbot ecology that has previously limited the ability of management agencies to plan and implement a suppression program.

Chapter two suggests that angler-supplied data collected from fishing tournaments targeting Burbot provide similar demographic rate estimates as data collected using fishery independent methods. As such, angling tournament may provide managers a cost-effective alternative for monitoring Burbot populations. However, if tournament data are used to monitor the response of a population to removal, occasional comparison of fishery-dependent data with fishery-independent data is warranted to ensure concordance between data types. Chapter three evaluated the demographics of Burbot in reservoirs of the Green River system. I also described the potential population growth response of Burbot in the reservoirs of the Green River to various management scenarios. Results indicate that substantially higher levels of exploitation are required to suppress lentic populations of Burbot than lotic populations of Burbot in the Green River. My findings suggest that the higher exploitation target of 33% should be used for removal of both river and reservoir populations. In chapter four, I used a combination of methods to describe the movement dynamics of Burbot in the upper Green River. Results suggest that a portion of the Burbot population exhibits an adfluvial life history. Fish movements were generally over short distances and spawning was suspected to occur in close proximity to Fontenelle Reservoir. The observed movement patterns may

benefit a suppression program because spawning areas are located in a relatively short section of river and may be a target for removal efforts.

Given the capacity of Burbot to negatively influence popular sport fisheries and native fish conservation efforts, a suppression program may be warranted. Although eradication of Burbot is not likely feasible, reducing the number of Burbot in the system is a tenable goal. A suppression program targeting Burbot will likely be an arduous process and require a substantial outlay of effort and funding. With the proper political impetus, such a program has the potential to be effective. The success of such a program will depend on the proper application of removal efforts. Unless effective methods for collecting juveniles are developed, mature Burbot should be targeted for removal. Through a combination of netting and angling, recruitment overfishing can be reached assuming the proper level of exploitation is reached. Additionally, by targeting spawning areas with these methods, the efficiency of removal efforts can be increased. To monitor the progress of a suppression program, angler-supplied data can be used as a cost-effective monitoring tool to reduce the overall cost of a sustained program.

Appendix A. Statement of author and coauthor contribution.

This thesis was the product of collaborative efforts between University of Idaho (UI) faculty, Idaho Cooperative Fish and Wildlife Research Unit (ICFWRU) personnel, and employees of the Wyoming Game and Fish Department (WGFD) and students attending the UI. I, Tucker Brauer, acted as principal investigator and lead author on all manuscripts resulting from this thesis. Co-authors and research committee members from the ICFWRU and UI provided editorial assistance and guidance regarding study design throughout the production of this thesis. Employees of WGFD assisted with data collection and provided insight into study design. All listed co-authors in this thesis have provided expertise and assistance that's warrants their inclusion as co-authors. As co-authors they have approved the work presented in this thesis.