

Population Ecology and the Suppression of Burbot in the Green River, Wyoming

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Authorization to Submit Thesis

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Abstract

Burbot in the Green River represent the only non-native Burbot population worldwide. The presence of Burbot is concerning for managers of the system due to the potential negative effects that Burbot may have on native and non-native fishes in the Green River. Therefore, managers of the Green River are interested in instigating a suppressing program for Burbot. This thesis sought to address knowledge gaps surrounding the ecology of Burbot to inform future suppression efforts of Burbot in the Green River. Specifically, I evaluated the efficacy of different sampling gears for Burbot. I also identified habitat characteristics that were most related to the presence and relative abundance of Burbot. Finally, I constructed an age-structured population model to better understand how Burbot in the Green River would respond to various management actions. Jointly, the objectives should contribute to the management of Burbot in the Green River and throughout their distribution.

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Dedication

This work is dedicated to Mike and Sandy Klein

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Chapter 1: General Introduction

Freshwater ecosystems are among the most vulnerable systems to invasions by introduced species (Marchetti et al. 2004). A general decline in freshwater biodiversity and an increase in native fishes imperilment can, in part, be attributed to the introduction of non-native fishes (Rahel 2002). Copp et al. (2005) reported that 185 freshwater non-native fishes have been introduced to the United States alone. Although introduced species have detrimental effects on native species (Gozlan 2008; McDowall 2006), human activity continues to assist the spread of non-native fishes worldwide for food aquaculture (51% of non-native introduction), the ornamental fish trade (21%), and recreational (12%) and commercial fisheries (7%; Gozlan 2008). Evidence suggests that a suite of factors (e.g., hydrological alterations, habitat loss, exploitation, pollution) contribute to a decline in biodiversity (Moyle and Williams 1990; Fu et al. 2003; Gozlan 2008); however, it is clear that invasive species play a substantial role in biodiversity decline and biotic homogenization (Rahel 2002; Cambray 2003; McDowall 2006).

Non-native species can have a number of effects on their recipient system that occur through a myriad of mechanisms, including predation (White and Harvey 2001; Taniguchi et al. 2002), hybridization (Scribner et al. 2001; Allendorf et al. 2004; McDonald et al. 2008; Muhlfeld et al. 2009), competition (Mills et al. 2004; McHugh and Budy 2005), and transmission of pathogens (Naylor et al. 2005; Gozlan et al. 2006). Negative effects on native species are often compounded because mechanisms are not independent and often co-occur. For example, invasive Common Carp *Cyprinus carpio* feed on both macroinvertebrates and macrophytes. Predation on invertebrates has a direct effect on macroinvertebrate biomass; whereas, consumption of macrophytes reduces habitat for invertebrates and thereby

(indirectly) decreases total macroinvertebrate biomass (Parkos III et al. 2003). While only about 1% of introduced species become problematic, the unknown effects (i.e., biotic and abiotic) of introduced species is a major concern for natural resource management agencies (Copp et al. 2005). For example, Burbot *Lota lota* were recently labeled as a “significant and immediate threat” in the Green River drainage, Wyoming, even though little is known about their ecology (Wyoming Game and Fish Department 2010).

Burbot are the only freshwater member of the family Gadidae (Howes 1991). They have a circumpolar distribution that rarely extends below 40°N, and occupy a diversity of lentic and lotic habitats throughout Europe, Asia, and North America (McPhail and Paragamian 2000). Across much of their distribution, Burbot populations have been extirpated or are declining, including populations in Eurasia (Tammi et al. 1999; Dillen et al. 2008; Stapanian et al. 2010), the contiguous U.S., and Canada (McPhail and Paragamian 2000; Stapanian et al. 2008 and 2010). However, Alaska, much of Canada, and select Eurasian countries (i.e., Latvia, Lithuania, Switzerland, and Russia) have stable Burbot populations (Evenson 2000; Stapanian et al. 2010). To my knowledge, the Green River drainage harbors the only illegally introduced Burbot population (Gardunio et al. 2011).

In Wyoming, Burbot are native to the Wind-Bighorn and Tongue River drainages, but have been extirpated from the Tongue River (Hubert et al. 2008; Gardunio et al. 2011). In the Wind-Bighorn River drainage, Burbot populations have declined due to exploitation and water diversions (Hubert et al. 2008). In the 1990s, Burbot were illegally introduced into Big Sandy Reservoir and began dispersing throughout the Green River drainage in the early 2000s (Gardunio et al. 2011). Since their introduction, Burbot have been sampled in the Green River drainage upstream of Fontenelle Reservoir in the New Fork River and south to

Dinosaur National Monument on the Utah-Colorado border (Gardunio et al. 2011). Although Burbot conservation is a focus in Wyoming, their illegal introduction into the Green River drainage raises concern regarding management of socially and economically important trout fisheries (i.e., Brown Trout *Salmo trutta*, Rainbow Trout *Oncorhynchus mykiss*, and Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus*). Additionally, Burbot in the Green River represent a threat to the conservation of native species including Bluehead Sucker *Catostomus discobolus*, Flannelmouth Sucker *Catostomus latipinnis*, Roundtail Chub *Gila robusta*. Therefore, natural resource management agencies are interested in implementing a suppression program for Burbot in the Green River drainage.

The control of non-native species can be categorized as prevention, early detection and eradication, and prolonged suppression (Peterson et al. 2009; Pyšek and Richardson 2010). Ideally, preventative methods should be used, but early detection and eradication is the most effective action when faced with non-native invasions. Early detection and eradication require constant monitoring which is complicated by species detection, funding, logistic constraints, and identification of the vulnerable areas (Chornesky and Randall 2003; Pyšek and Richardson 2010). For many introduced species, the only choice is long-term suppression programs that attempt to maintain non-native species at low abundance (Simberloff 2003; Mueller 2005).

Programs focused on suppression of non-native species are generally time consuming and costly; thus, designing efficient programs is critically important for natural resource agencies (Pimentel et al. 2005; Baxter et al. 2007; Berthou 2007). Because of the associated cost, effective suppression programs should attempt to reach a balance between effort, cost, and exploitation. Unfortunately, the paucity of information on the ecology of Burbot limits

natural resources management agencies' ability to implement a cost effective suppression strategy for Burbot in the Green River. More specifically, relatively little is known about effective gears for sampling Burbot. Even if effective gears are identified, questions regarding the habitat use of Burbot remain. Without a clear understanding of the habitat use of Burbot the efficacy of any removal effort will be severely constrained. Finally, relatively little is known about the demographics of Burbot in the southern extent of the species distribution, making inferences on the population level response to management actions tenuous.

Given the considerable knowledge gaps associated with the management of Burbot, this thesis had three main objectives. The first objective was to identify effective and efficient sampling gears for Burbot. Secondly, the relationship between habitat characteristics and the presence and relative abundance of Burbot in the Green River was investigated. Finally, demographic data were used to construct an age-structured population model that would allow for the evaluation of how the Burbot population in the Green River would respond to different management scenarios.

Thesis Organization

This thesis is composed of five chapters. The second chapter compares the effectiveness of small-mesh hoop nets, large-mesh hoop nets, and night electrofishing for sampling Burbot in a lotic system. Chapter two has been accepted for publication in *Fisheries Management and Ecology*. The third chapter investigates the relationship between habitat characteristics and the occurrence and relative abundance of Burbot and has been accepted for publication in *Hydrobiologia*. Chapter four evaluates how the Burbot population in the Green River is likely to respond to different management actions. The fourth chapter will be

submitted to the *North American Journal of Fisheries Management*. The final chapter is a general conclusion that synthesizes the results of each chapter as they relate to the management of Burbot in the Green River, Wyoming.

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Chapter 2: Sampling Techniques for Burbot in a Western Non-Wadeable River

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Abstract

Burbot, *Lota lota* (Linnaeus), populations are declining throughout much of their native distribution. Although numerous aspects of Burbot ecology are well understood, less is known about effective sampling techniques for Burbot in lotic systems. Occupancy models were used to estimate the probability of detection (\hat{p}) for three gears (6.4- and 19-mm bar mesh hoop nets, night electric fishing), within the context of various habitat characteristics. During the summer, night electric fishing had the highest estimated detection probability for both juvenile (\hat{p} , 95% C.I.; 0.35, 0.26–0.46) and adult (0.30, 0.20–0.41) Burbot. However, small-mesh hoop nets (6.4-mm bar mesh) had similar detection probabilities to night electric fishing for both juvenile (0.26, 0.17–0.36) and adult (0.27, 0.18–0.39) Burbot during the summer. In autumn, a similar overlap between detection probabilities was observed for juvenile and adult Burbot. Small-mesh hoop nets had the highest estimated probability of detection for both juvenile and adult Burbot (0.46, 0.33–0.59); whereas, night electric fishing had a detection probability of 0.39 (0.28–0.52) for juvenile and adult Burbot. By using detection probabilities to compare gears, the most effective sampling technique can be identified, leading to increased species detections and more effective management of Burbot.

Introduction

Effective management of fish requires reliable information on their population dynamics and demographics (Allen & Hightower 2010). Obtaining this information depends on techniques that are both effective and efficient at sampling target species. However, evaluating the efficacy of a given gear is often labour intensive. Furthermore, the effectiveness of a given gear likely varies when that technique is applied to a novel species or

habitat (Schloesser *et al.* 2012). Without a clear understanding of the biases associated with a particular sampling technique and how those biases vary with biotic (e.g. fish behaviour, species interaction) and abiotic (e.g. environmental characteristics) factors, inferences about the target species may result in ineffective or incorrect management decisions.

A number of metrics are available to evaluate sampling techniques (e.g. density, presence-absence). Catch rate is commonly used to examine the sampling efficiency of gears, but requires non-zero catch rates for meaningful conclusions (Quist *et al.* 2006). When catch rates are low, counts are often unreliable and must be combined with an estimate of detection to evaluate the biases of a sampling method (MacKenzie *et al.* 2002). Because a species can be present, absent or present but undetected, detectability (the probability of being detected) must be accounted for in an analysis or inference regarding changes in the status of a species can potentially be misleading (MacKenzie *et al.* 2002, 2006). Gear comparisons are often avoided because traditional estimates of detection (e.g. mark-recapture, depletion) are effort intensive. Instead, the least selective gear or multiple gears are used to reduce the effect of gear bias (Beamesderfer & Riemen 1988). However, the use of a less selective gear or multiple gears assumes perfect detection and ignores variations in detectability. Additionally, because the effort of passive (e.g. hoop nets, trammel nets) and active (e.g. electric fishing) sampling techniques varies, direct comparisons of efficacy between passive and active gears are notoriously difficult (Peterson & Paukert 2009; Hubert *et al.* 2012). Effective management of a species is dependent on being able to reliably sample that species. Therefore, understanding variations in detectability and the factors that influence detectability is integral to the effective implementation of a given sampling technique (Jensen & Vokoun 2013).

Burbot, *Lota lota* (Linnaeus), is the only freshwater member of the family Gadidae (Howes 1991). It has a circumpolar distribution that rarely extends below 40°N and occupies a diversity of lentic and lotic habitats throughout Eurasia and North America (McPhail & Paragamian 2000). Stable Burbot populations exist in Alaska, much of Canada and several Eurasian countries including Latvia, Lithuania, Switzerland and Russia (Stapanian *et al.* 2010). However, across much of its distribution, Burbot are declining or have been completely extirpated, including populations in Eurasia, Canada and the contiguous USA (Tammi *et al.* 1999; McPhail & Paragamian 2000; Dillen *et al.* 2008; Stapanian *et al.* 2008, 2010). Although Burbot conservation is a major focus around the world, basic questions remain regarding the most effective technique for sampling Burbot.

In Wyoming, Burbot are a concern not only because of declines in their native distribution but also because of their illegal introduction outside of their native distribution within the state. Burbot are native to the Wind-Bighorn River and Tongue River drainages in northern Wyoming but have been extirpated from the Tongue River basin (Hubert *et al.* 2008; Gardunio *et al.* 2011). In the Wind-Bighorn River system, Burbot populations have declined due to angler exploitation and water development (Hubert *et al.* 2008). In the 1990s, Burbot were illegally introduced outside of their native distribution into Big Sandy Reservoir and began dispersing throughout the Green River drainage in the early 2000s (Gardunio *et al.* 2011). Since their introduction, Burbot have been sampled upstream of the confluence of the New Fork and Green rivers downstream to Dinosaur National Monument on the Utah-Colorado border (Gardunio *et al.* 2011). Although Burbot conservation is a focus in the Wind-Bighorn River drainage, their introduction to the Green River system raises concern regarding management of socially and economically important trout fisheries [i.e. brown

trout, *Salmo trutta* Linnaeus, rainbow trout, *Oncorhynchus mykiss* (Walbaum) and Colorado River cutthroat trout, *Oncorhynchus clarkii pleuriticus* (Richardson)], and conservation of native non-game fishes [i.e. bluehead sucker, *Catostomus discobolus* Cope, flannelmouth sucker, *Catostomus latipinnis* Baird & Girard and roundtail chub, *Gila robusta* Baird & Girard (Gardunio *et al.* 2011)]. Additionally, the fact that Burbot are not native, yet abundant, in the Green River facilitates research that would otherwise be limited by low numbers of Burbot in other areas of their native distribution.

Burbot have been sampled using a variety of techniques (e.g. hoop nets, gill nets, electric fishing). However, little research has focused on comparing the effectiveness of different techniques in lotic and lentic habitats. The majority of studies focused on evaluating the effectiveness of sampling techniques for Burbot have occurred in lentic systems using passive gears (Bernard *et al.* 1991; Spence 2000; Prince 2007). Although many of these studies used similar sampling techniques, drawing general conclusions is difficult due to inconsistent results. For example, Bernard *et al.* (1991) concluded that hoop nets were effective at capturing Burbot in central Alaskan lakes. In contrast, Prince (2007) reported that cod traps had higher catch rates of Burbot than hoop nets in Moyie Lake, British Columbia. Confounding general conclusions further, catch rates for trammel nets were nearly double those of hoop nets and cod traps in Boysen Reservoir, Wyoming (A. Dux, Idaho Department of Fish and Game, unpublished data). Results from gear comparisons in lotic systems for Burbot are equally inconclusive. For example, Horton & Strainer (2008) compared slat traps, cod traps and hoop nets in the Missouri River, Montana, but found little difference in catch rates across gears. Bernard *et al.* (1991) compared large- and small-diameter hoop nets using the same mesh size (i.e. 25-mm bar mesh) as Horton & Strainer (2008) and found that larger

diameter hoop nets had higher catch rates than small diameter hoop nets. Although direct comparisons between hoop nets used in lotic systems is difficult due to myriad configurations (e.g. diameter, mesh size), the conflicting results demonstrate the need to further evaluate hoop nets for sampling Burbot. In addition, inconsistent results from studies comparing passive gears highlight the need to evaluate different sampling techniques for Burbot in lotic systems.

Given conservation concerns surrounding Burbot and the lack of information on the most effective techniques for sampling them, the objective of this study was to compare the detection probability (\hat{p}) of small-mesh hoop nets (i.e. 6.4-mm bar mesh), large-mesh hoop nets (i.e. 19-mm bar mesh) and night electric fishing for juvenile and adult Burbot in the Green River drainage of Wyoming using occupancy modelling. An additional objective was to investigate the effect that habitat characteristics (i.e. dominant substrate, current velocity, depth, in-stream cover, bank type and water temperature) had on the probability of detection.

Study Site

The Green River is the largest tributary of the Colorado River and drains portions of Wyoming, Utah and Colorado (Fig. 1; Wyoming Game and Fish Department 2010). The Green River originates in the Wind River Range of western Wyoming and flows for approximately 235 km before entering Fontenelle Reservoir. From Fontenelle Reservoir, the Green River flows for about 150 km until it enters Flaming Gorge Reservoir at the Wyoming-Utah border. Upstream of Fontenelle Reservoir, the Green River is characterised by high gradient runs interspersed with pool-riffle habitat and substrate characteristics of alluvial deposits (e.g. cobble, gravel, sand and silt; Kurtz 1980). From Fontenelle Dam to its

confluence with the Big Sandy River, the Green River is characterised by long runs averaging 450 m (Wiley 1974). After its confluence with the Big Sandy River, the Green River is relatively low-gradient and the substrate is dominated by sand and gravel substrate (Wiley 1974). Most of the Green River basin is characteristic of a high desert climate with monthly temperature averages of -9°C (January) and 17°C (July) and low annual precipitation (25.4 cm; Wyoming Game and Fish Department 2010).

Methods

Sampling was conducted in four river sections during summer (22 May – 12 July 2013) and two river sections during autumn (6 – 25 September 2013). Sections were not a unit of interest per se; rather, they were simply used to allocate sampling effort. Sections were selected to ensure habitat was representative of the Green River. Each section was divided into 150-m long sites. In total, 49 sites were randomly selected for sampling ($n = 41$ in summer; $n = 28$ in autumn; Fig. 2.1). All sites were sampled with small- and large-mesh hoop nets (6.4-mm and 19-mm bar mesh, respectively) and night electric fishing. Sites were sampled over a 9-day period such that each site was sampled three times with each sampling gear. For example, on day one a given site was sampled with a randomly selected small- or large-mesh hoop net. The following day the site was sampled using the size of hoop net not used the previous day. The site was sampled using night electric fishing on the final day to avoid biasing hoop net detections. Three days of consecutive sampling events was considered a sampling occasion, and each site was sampled on three occasions per season. The summer sampling season commenced at the most downstream section and continued upstream until all sites had been sampled in triplicate. To increase sample size during autumn, 19 sites were

added to the 41 sites sampled in the summer. However, due to unusually high precipitation and logistical constraints, only the most upstream sites ($n = 15$; section 1, Fig. 2.1) and the sites immediately downstream of Fontenelle Dam ($n = 13$; section 3) were sampled during autumn.

The small-mesh hoop nets had seven 0.6-m diameter hoops and an overall length of 3 m. A fish “escape route” was installed between the sixth and seventh hoop to allow fish to escape from of a lost net. “Escape routes” consisted of a 20 cm \times 20 cm square opening covered with 6.4-mm bar mesh secured with 3-mm untreated cotton twine. The large-mesh hoop nets had four 0.91-m diameter hoops and an overall length of 2.9 m. Each net had a “Mammalian Escape Hatch” placed between the third and fourth hoop, consisting of a 20 cm \times 41 cm square opening covered with a 36 cm \times 61 cm square section sewn on three sides (A. Senecal, Wyoming Game and Fish Department, unpublished information). Each net was positioned parallel to the current with the cod end anchored upstream. Nets were baited with white sucker, *Catostomus commersonii* (Lacepède), a non-game, non-native species in the system and fished for 24 h.

Night electric fishing was conducted using a drift boat equipped with a 5,000 W generator and Smith-Root VVP-15B electrofisher (Smith-Root, Vancouver, WA). Electric fishing power output was standardised to 2,750 – 3,200 W with a duty cycle of 45% and a frequency of 45 Hz (Miranda 2009). One netter was positioned on the bow of the boat using a 2.4-m long dip net with 6-mm bar knotless mesh. Electric fishing proceeded downstream from the upstream most point of each 150 m site. Fish were enumerated, weighed (g) and measured for total length (mm). Effort was recorded as the total number of seconds electricity was applied to the water.

Six site-specific habitat variables (i.e. current velocity, depth, wetted width, dominant substrate, in-stream cover and bank type) that were hypothesised to affect the probability of occupancy and detectability were measured once per season at each site. Channel units (i.e. riffle, run, pool) were sampled separately for habitat characteristics. Channel-unit length and width were measured to the nearest 0.5 m using a laser rangefinder. Sites with a single channel-unit type were divided in half by length, and each half was treated as a channel unit. In-stream habitat characteristics were measured along a transect that ran diagonally from the upper-most point of the channel unit to the lower-most point of the channel unit on the opposite bank. In-stream habitat characteristics (i.e. current velocity, dominant substrate, in-stream cover and depth) were measured at 20, 40, 50, 60 and 80% of the transect's length (Flotemersch *et al.* 2006; Sindt *et al.* 2012). Depth was measured using a 2 m sounding pole or a portable electronic depth finder (Marcum LX-i, Minnetonka, MN). Current velocity was measured using a portable flow meter (Flo-Mate Model 2000; Marsh-McBirney, Loveland, CO). The dominant substrate was visually estimated as organic matter-silt (< 0.262 mm), sand and gravel (0.263 – 64.0 mm), cobble (64.0 – 256.0 mm), boulder (> 256.0 mm), or bedrock (modified from Orth & Maughan 1982). Presence or absence of cover (i.e. large woody debris, overhanging vegetation, undercut banks, boulders, macrophytes and man-made structures) was recorded at each transect point (Fitzpatrick *et al.* 1998; Neebling & Quist 2010). The proportion of each bank type (i.e. alluvium and vegetation, eroded, undercut, vegetation, boulder, anthropogenic structure, woody debris and sand and gravel) was visually estimated for each site. An additional bank type called “alluvium bluff” was estimated for each site and was characterised by steep, eroded banks with large substrate (≥ 64.0 mm; modified from Jaeger *et al.* 2005). In addition to site-specific habitat variables, sample-

specific habitat variables [i.e. temperature ($^{\circ}\text{C}$), conductivity ($\mu\text{S cm}^{-1}$), Secchi depth (m)] thought to affect occupancy and detection probabilities were measured at each sampling event following fish sampling.

Length structure was assessed for each sampling technique for Burbot in the Green River for summer and autumn (2013) using length-frequency histograms (Fig. 2.2). Although gear-specific size selectivity was not a primary focus of this study, length-structure information provided valuable insight for the management of Burbot.

Occupancy modelling was used to estimate the detection and occupancy probability of each sampling gear for juvenile and adult Burbot for the summer and autumn. Single-season, single-species occupancy models were constructed using programme PRESENCE (Hines 2006). Single-season, single-species models were chosen because they directly addressed our research questions and their simple form allowed for inclusion of multiple covariates.

Programme PRESENCE estimates both the probability of a site being occupied (Ψ) and the probability of a species being detected at an occupied site (\hat{p}) using the detection history of repeatedly sampled sites. Detection histories represent the detection or non-detection of a species at a series of sampling events. A sampling occasion was then represented by the detection history of three independent sampling events and a season was represented by three sampling occasions. Because a species can either be present, absent or present but undetected at a site, PRESENCE uses the detection history to estimate the probability of detection at a site known to be occupied during a single sampling event within a sampling occasion.

Occupancy is then the probability that a species is present at a site and requires a single positive detection to estimate (MacKenzie *et al.* 2005; 2006). Although obtaining estimates of detectability was the primary focus of this study, it was necessary to model occupancy by

season and habitat to acquire the best model fit (MacKenzie & Bailey 2004). The estimates of the probability of detection (\hat{p}) were used as an index for comparing sampling techniques (Schloesser *et al.* 2012; Haynes *et al.* 2013). Additionally, site- and sample-specific covariates were added to occupancy models to explain variability in detection by season and gear for juvenile and adult Burbot.

Mean depth, current velocity, substrate composition and bank type were hypothesised to be the primary factors affecting the probability of detecting Burbot (Dixon & Vokoun 2009; Eick 2013; Table 2.1). Flaming Gorge and Fontenelle reservoirs were hypothesised to act as thermal refugia for Burbot during periods of high mean water temperature and as a “source” of Burbot. Therefore, a covariate of river kilometre (rkm) between sites and the downstream reservoir was included.

A Spearman’s rank-order correlation coefficient was used to assess multicollinearity amongst covariates (Higgins 2003; Sindt *et al.* 2012). If two covariates were highly correlated ($|\rho| > 0.70$), only the most ecologically important and interpretable variable was used in candidate models (Burnham & Anderson 1998). For example, mean depth was highly correlated with maximum depth ($|\rho| > 0.85$); mean depth was used because it better represented depth of the overall site.

Gear-specific detection probability (detectability) was investigated using a multi-step approach. First, the probability of occupancy was estimated within the context of covariates hypothesised to influence occupancy, while the detectability parameter was held constant (Smith 2013). Each of these models was ranked using Akaike’s Information Criterion adjusted for small sample size (AIC_c ; Burnham & Anderson 1998). The occupancy model with the lowest AIC_c value was then used to estimate the probability of detection for each

gear. Again, estimates of occupancy were not the direct focus in this study. Rather, the best estimate of occupancy was needed so the occupancy component of the model could be held constant while \hat{p} was estimated. Detection probabilities of each sampling technique were estimated using a gear-specific model without including covariates. Gear-specific models consistently had more support (i.e. lower AIC_c value) than models with constant detection. Therefore, the influence of habitat characteristics on the detectability of each gear was evaluated using gear-specific detectability models. To address changes in detectability by gear, gear-specific models included interactions with habitat covariates. Because habitat characteristics likely influence life history stages differently, juvenile and adult Burbot detections were modelled separately for the summer samples (juvenile < 280 mm; adult ≥ 280 mm; Amundsen *et al.* 2003). Due to low catch rates and a shortened sampling period, it was necessary to pool juvenile and adult Burbot detections during autumn. To facilitate a more direct comparison of detection probabilities between the summer and fall, juvenile and adult Burbot detections from the summer were also pooled. Because Fontenelle Dam acts a barrier to fish movement, the upper (sections 1 and 2) and lower (sections 3 and 4) portions of the river were considered separate for modelling. An overdispersion parameter (\hat{c}) was estimated for all models using a Pearson chi-square statistic and parametric bootstrap (1,000 iterations). The \hat{c} from the most parameterised model within the suite of candidate models was used to adjust estimated model variance for overdispersed models ($\hat{c} > 1$; Burnham & Anderson 1998; MacKenzie *et al.* 2006). If models were overdispersed, quasi- AIC_c ($QAIC_c$) was used to rank the models, and an additional parameter was added to further penalise candidate models (Burnham & Anderson 1998). All models with a ΔAIC_c or $\Delta QAIC_c$ of ≤ 2 were considered plausible (Burnham & Anderson 1998; Schloesser *et al.* 2012).

Results

Substrate, bank composition and Secchi depth varied little amongst sites within a section but were highly variable between river sections and seasons (Table 2.1). For example, the most downstream sites (section 4) averaged 12% (SE = 0.06) large substrate (cobble and boulder); whereas, sites immediately downstream of Fontenelle Dam (section 3) averaged 83% (SE = 0.09) large substrate. Similarly, an overall difference of 64% alluvium and vegetated bank was apparent between sites directly upstream of Flaming Gorge Reservoir (section 4) and sites immediately downstream of Fontenelle Dam (section 3). Depth and current velocity were relatively homogenous throughout the Green River. A difference of only 0.24 m in mean depth was observed during the summer between the shallowest (mean depth \pm SE; 0.89 ± 0.06 m) and deepest (1.13 ± 0.05 m) sections sampled. Current velocity exhibited similarly low variability. For instance, current velocity differed by only 0.22 m s^{-1} between sites directly downstream of Fontenelle Dam (highest mean current velocity) and sites immediately upstream of Flaming Gorge Reservoir (lowest mean current velocity) during the summer.

Length structure of Burbot in the Green River increased for all gears from the summer to autumn. Additionally, the mean length of Burbot sampled by all gears increased from the summer (mean length \pm SE; 333.4 ± 8.9 mm) to autumn (435.7 ± 10.4 mm; Fig. 2.2). The greatest range of lengths of Burbot was collected with night electric fishing for both seasons.

During the summer, 118 Burbot were sampled using small-mesh hoop nets ($n = 38$ Burbot), large-mesh hoop nets ($n = 10$ Burbot) and night electric fishing ($n = 70$ Burbot). Adult Burbot were detected at 25 of the 41 sites, and juvenile Burbot were detected at 29 of the 41 sites. Models including gear-specific effects on detection probabilities had clear

support for juvenile and adult Burbot (Table 2.2). None of the top models from each suite of candidate models from the summer (i.e. juveniles, adults and pooled) contained habitat covariates. Probability of detection of adult Burbot in the summer was lowest with large-mesh hoop nets (Table 2.3). Night electric fishing and small-mesh hoop nets had similar probabilities of detection for adult Burbot. The probability of detection for juvenile Burbot using night electric fishing and small-mesh hoop nets were similar during the summer. Detectability of juvenile Burbot was similar to that of adult Burbot for all gears during the summer.

A total of 112 Burbot was captured during autumn using small-mesh hoop nets ($n = 53$ Burbot), large-mesh hoop nets ($n = 13$ Burbot) and night electric fishing ($n = 46$ Burbot). Adult Burbot were detected at 20 of the 28 sites and juvenile Burbot were detected at 5 of the 28 sites. In autumn, the probability of detection of juvenile and adult Burbot was similar for small-mesh hoop nets (Table 2.3) and night electric fishing. Although there was an overall increase in detection probability during autumn compared to summer, large-mesh hoop nets continued to have the lowest probability of detection. Along with gear type, models containing proximity to downstream reservoir had the most support (Table 2.2). When controlling for upper and lower sections, the proximity to downstream reservoir negatively influenced the probability of detection for all gears (Table 2.4).

Discussion

A gear-specific effect on detection probabilities was apparent for juvenile and adult Burbot for both seasons. The effect of gear on detection probabilities was not surprising given the long-established biases associated with different fish sampling techniques (Paukert

2004; Hetrick & Bromaghin 2010). For instance, Schloesser *et al.* (2012) reported that detection probabilities for a number of Missouri River fishes were most influenced by sampling technique (i.e. gill net, trammel net, otter trawl). Similarly, Beamesderfer & Riemen (1988) found a species-specific pattern of size-selectivity for largemouth bass, *Micropterus salmoides* (Lacepède), walleye, *Sander vitreus* (Mitchill), and northern pikeminnow, *Ptychocheilus oregonensis* (Richardson), in John Day Reservoir, Oregon using traps nets, electric fishing, angling and two sizes of monofilament gill nets. In the current study, length frequencies indicated that night electric fishing was the least size-selective gear. A number of factors have been identified as influencing gear biases including biological, technical and environmental characteristics (Reynolds & Kolz 2012). The effect of environmental factors on gear bias was accounted for by including habitat characteristics in occupancy models. However, the current study did not assess the technical and biological factors influencing gear bias. Without further research, it is difficult to assess all the constituents that influence the vulnerability of Burbot to a given gear. Regardless, the findings of the current study highlight the need to better understand the biases and variations in detectability of both active and passive gears for sampling Burbot.

Only one other study has evaluated both passive and active sampling techniques for Burbot in lotic systems. Smith (2013) sampled Burbot in the Kootenai River, Idaho and the Green River, Wyoming using day electric fishing and 6.4-mm bar mesh hoop nets as part of a larger fish assemblage study. Smith (2013) reported that detection probabilities ($\hat{p} \pm SE$; 0.19 ± 0.14) for juvenile Burbot were identical between 6.4-mm bar mesh hoop nets and day electric fishing. However, detection probabilities for adult Burbot were quite different between day electric fishing (0.12 ± 0.09) and 6.4-mm bar mesh hoop nets (0.61 ± 0.14).

Although the detection probabilities for juvenile and adult Burbot using 6.4-mm bar mesh hoop nets from this study were different from Smith (2013), direct comparisons are tenuous given disparate sampling designs between the two studies. Specifically, Smith (2013) set four 6.4-mm bar mesh hoop nets at each sampling event for 12 h and pooled detections of Burbot; whereas, a single 6.4-mm bar mesh hoop net was set for 24 h per sampling event in the current study. The addition of three nets per site likely influenced the detection probabilities reported by Smith (2013). Smith (2013) reported much lower detection probabilities using day electric fishing compared to the results for night electric fishing from the current study. No studies have specifically compared day and night electric fishing for Burbot. However, previous research has reported higher catch rates and greater species diversity using night electric fishing compared to day electric fishing (Sanders 1992; Pierce *et al.* 2001; McNerny & Cross 2004). The disparity in catch rates between day and night electric fishing is likely due to differences in the ecology of the study species. For example, Sanders (1992) reported collecting approximately double the number of flathead catfish, *Pylodictis olivaris* (Rafinesque), in the Ohio and Muskingum rivers using electric fishing at night compared to the day. Flathead catfish are reported as being largely inactive during the day and exhibiting greater movement and feeding during the dusk, night and dawn (Vokoun & Rabeni 2006; Daugherty & Sutton 2005). Burbot are similarly inactive during the day but begin foraging at dusk and continue until dawn (Carl 1995). Additionally, Burbot often use large substrates as cover during periods of inactivity (Dixon and Vokoun 2009; Eick 2013), which may reduce their vulnerability to capture by electric fishing (Reynolds & Kolz 2012). The sedentary behaviour of Burbot coupled with their affinity for large substrate habitats likely accounts for decreased detectability observed with day electric fishing.

Models including covariates for habitat were not strongly supported using data from the summer. However, proximity to downstream reservoir negatively influenced the detection probability of all gears during autumn. The relationship between gears and proximity to downstream reservoir may be related to pre-spawning movement exhibited by adfluvial Burbot. Adfluvial populations of Burbot occur in eastern North America, northern latitudes of the Missouri River system and the Kootenai River system of Idaho and British Columbia (Paragamian 2000; Hubert *et al.* 2008). Many adfluvial Burbot populations undergo pre-spawning movement in autumn (Lawler 1963). Pre-spawning movement of Burbot in the Green River likely coincided with autumn sampling as evidenced by the increased mean length of Burbot and higher relative abundance. For instance, 64 juvenile and adult Burbot averaging 379.3 mm were caught in section 1 during the fall compared to 31 juvenile and adult Burbot averaging 287.5 mm caught in section 1 during the summer. Because detectability is often positively related to site-specific abundance (Royle & Nichols 2003), sampling conducted at sites closer to source reservoirs likely resulted in increased detection probabilities.

Occupancy modelling provided a useful framework to compare active and passive sampling techniques while accounting for the potential influence of habitat characteristics on detectability. Night electric fishing and small-mesh hoop nets had similar detection probabilities for juvenile and adult Burbot in the Green River; however, night electric fishing required substantially less effort. Although night electric fishing is possible in many western systems, safety considerations of working at night will likely preclude its use in many river systems. Additionally, electric fishing efficiency decreases with increasing water depth (Reynolds & Kolz 2012). In situations where electric fishing is not possible, small-mesh

hoop nets may be a suitable alternative. Not only are hoop nets effective at sampling deep habitats, but concerns of working in a lotic system at night can be avoided in that hoop nets can be set during the day. Regardless of the sampling technique employed, it is important to note that given the prevalence of adfluvial populations of Burbot in many rivers, sampling conducted in autumn will likely be more effective than in other seasons. By using night electric fishing, small-mesh hoop nets, or a combination of the two, Burbot can be efficiently and effectively monitored in lotic systems characteristic of the western USA.

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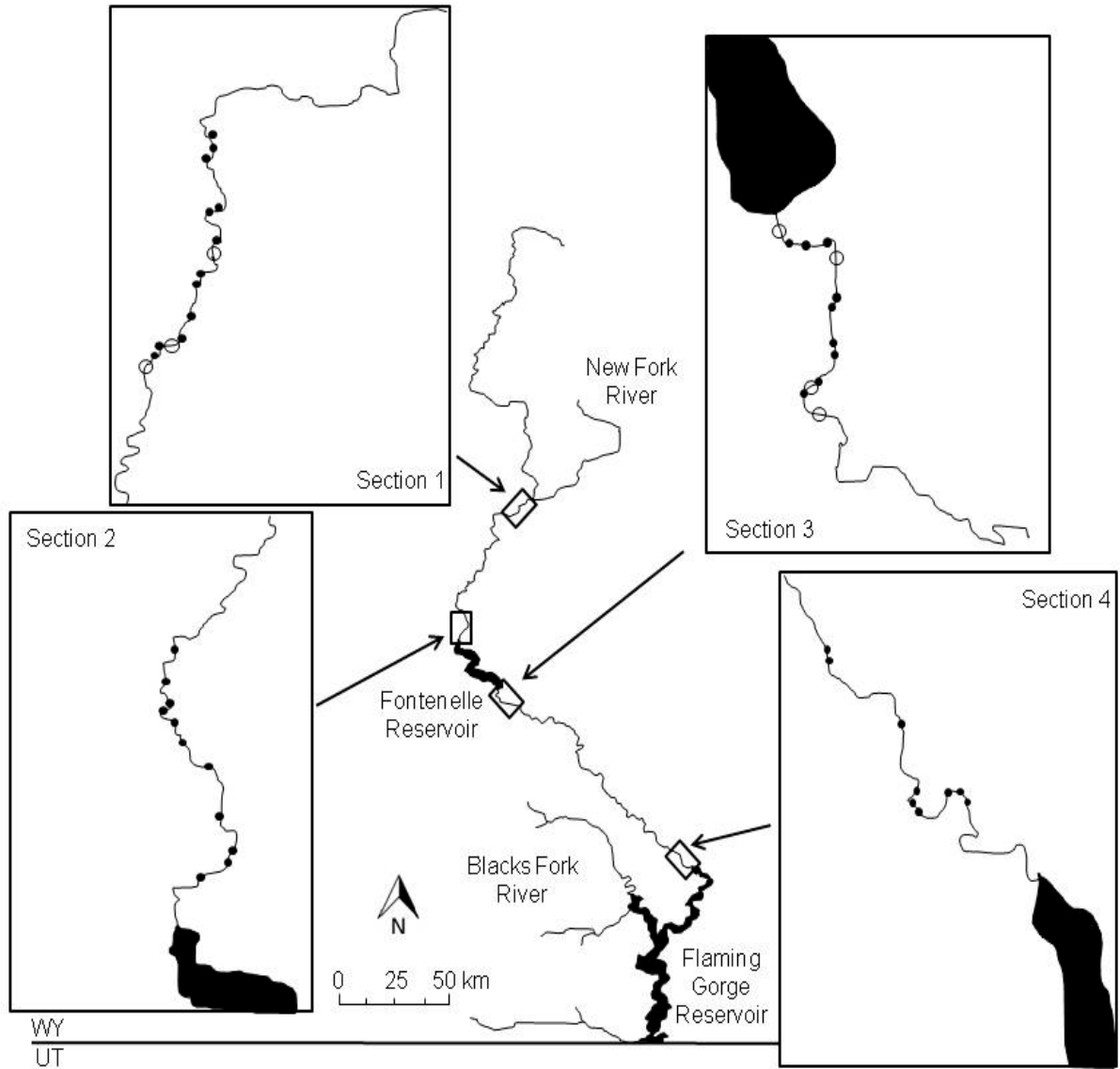


Figure 2.1. Sections used for Burbot sampling in the Green River, Wyoming during the summer and autumn (2013). Boxes depict each section in detail, with sites sampled in the summer (solid black circles) and sample sites added in autumn to increase sample size (open black circles).

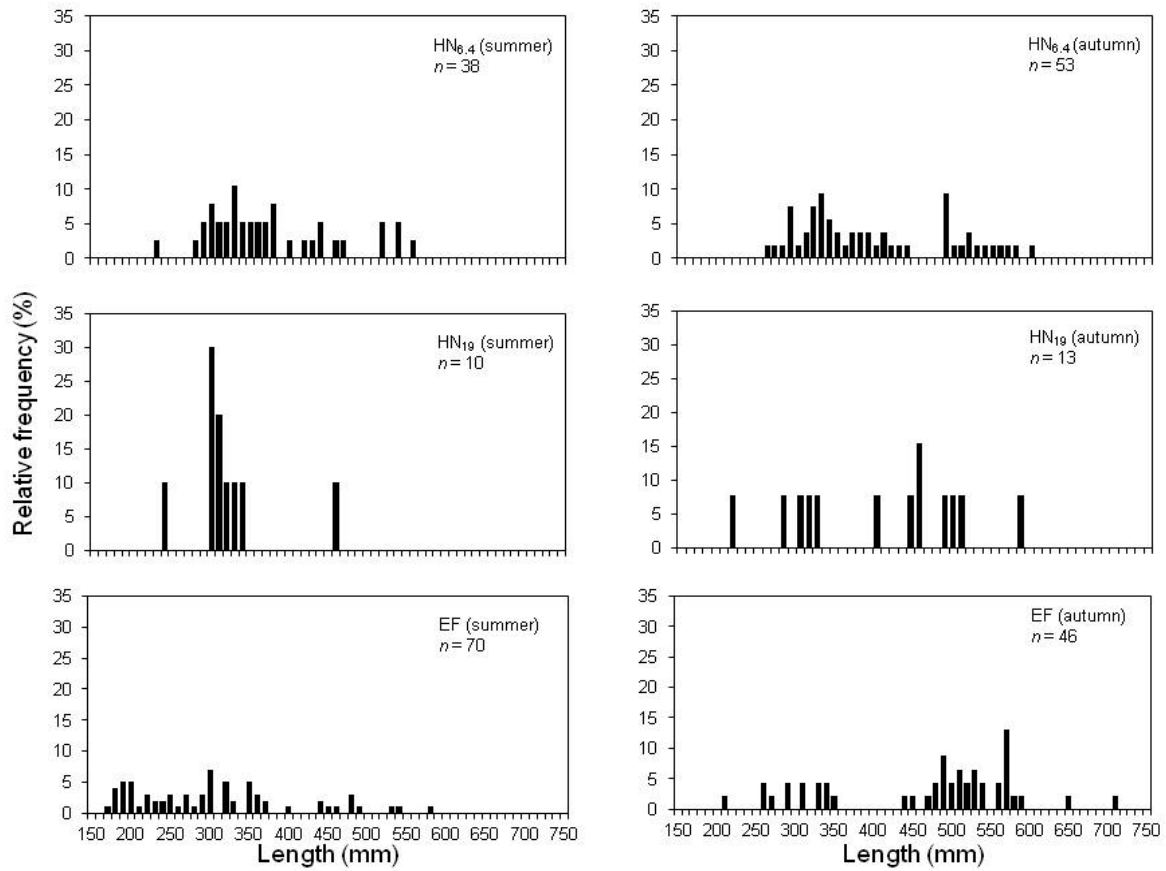


Figure 2.2. Length-frequency histograms for 6.4-mm bar measure mesh hoop nets (HN_{6.4}), 19-mm bar measure mesh hoop nets (HN₁₉), and night electrofishing (EF) for juvenile and adult Burbot sampled in the Green River of Wyoming during the summer and autumn (2013).

Table 2.1. Mean and standard error (in parenthesis) of site- and sample-scale (indicated by asterisk) variables used to evaluate detection probabilities for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). River section 1 is the most upstream section followed by sections 2, 3, and 4.

Variable	Description	Summer				Autumn	
		Section 1	Section 2	Section 3	Section 4	Section 1	Section 3
Depth _{CV}	Mean coefficient of variation of depth	0.36 (0.02)	0.38 (0.02)	0.31 (0.02)	0.34 (0.04)	0.31 (0.02)	0.30 (0.02)
Depth _{Mean}	Mean depth	1.13 (0.05)	0.94 (0.02)	0.93 (0.03)	0.96 (0.10)	0.89 (0.06)	1.01 (0.06)
Velocity _{CV}	Mean coefficient of variation of water column velocity	0.31 (0.03)	0.39 (0.06)	0.36 (0.06)	0.46 (0.07)	0.46 (0.05)	0.41 (0.05)
Velocity _{Mean}	Mean water column velocity (m/s)	0.60 (0.03)	0.55 (0.05)	0.61 (0.09)	0.39 (0.05)	0.40 (0.04)	0.45 (0.04)
Proximity	Distance from downstream reservoir (rkm)	46.86 (1.20)	8.77 (1.71)	120.70 (0.58)	8.72 (1.23)	46.28 (1.04)	120.60 (0.58)
*Temp	Temperature for each sampling event (C°)	19.94 (0.16)	18.80 (0.11)	14.65 (0.09)	16.07 (0.24)	16.19 (0.17)	17.10 (0.12)
Secchi _{Mean}	Mean Secchi disk depth (m)	0.63 (0.00)	0.72 (0.03)	0.83 (0.00)	0.61 (0.04)	0.46 (0.02)	0.93 (0.00)
Substrate _{Co-} BI	Proportion of cobble and boulder substrate	0.53 (0.10)	0.81 (0.08)	0.83 (0.09)	0.12 (0.06)	0.63 (0.06)	0.93 (0.06)
Substrate _{BI}	Proportion of boulder substrate	0.08 (0.04)	0.01 (0.01)	0.06 (0.06)	0.02 (0.02)	0.07 (0.03)	0.21 (0.03)
Bank _{Veg}	Proportion of vegetated bank	0.51 (0.07)	0.50 (0.08)	0.07 (0.04)	0.41 (0.12)	0.42 (0.06)	0.16 (0.06)
Bank _{AV}	Proportion of alluvium - vegetated bank	0.03 (0.02)	0.13 (0.05)	0.64 (0.10)	0.00 (0)	0.19 (0.06)	0.48 (0.06)
Bank _{Bluff}	Proportion of alluvium bluff bank	0.14 (0.06)	0.14 (0.07)	0.15 (0.07)	0.29 (0.08)	0.17 (0.06)	0.22 (0.06)
Bank _{Eroded}	Proportion of eroded bank	0.40 (0.05)	0.33 (0.05)	0.31 (0.09)	0.48 (0.09)	0.37 (0.07)	0.33 (0.07)
Mp	Proportion of in-stream macrophyte cover	0.36 (0.09)	0.85 (0.07)	0.63 (0.13)	0.72 (0.11)	0.30 (0.04)	0.57 (0.04)
*Effort	Total number of minutes for each sampling event (Min)	870.10 (6.65)	906.40 (3.19)	892.10 (4.48)	933.60 (11.25)	928.90 (2.70)	957.60 (2.70)

Table 2.2. Candidate models used to evaluate the influence of site- and sample-scale covariates on occupancy (Ψ) and detection probability (\hat{p}) for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). Only models with a $\Delta AIC_c < 2$ and the most parameterized model (indicated in bold font) in each candidate set are included. Akaike's Information Criterion (AIC_c) adjusted for small sample size or quasi-Akaike's Information Criterion ($QAIC_c$) adjusted for overdispersion was used to rank all candidate models. Models ranked using $QAIC_c$ are indicated with an asterisk. Model weight (w_i) and total number of parameters (K) are also included. The relationship of covariates with detectability is indicated as positive (+) or negative (-).

Season and life history stage	Model name	AIC_c or $QAIC_c$	ΔAIC_c or $QAIC_c$	w_i	K
Summer					
	Adult	Ψ (Bank _{Eroded}), \hat{p} (Gear, -Section)	*160.26	0.00	0.45
	Ψ (Bank_{Eroded}), \hat{p} (Gear, +Temp, -Effort, -Velocity_{Mean})	*168.83	8.57	0.00	11
	+Section				
Juvenile	Ψ (-Proximity), \hat{p} (Gear, -Section)	*175.01	0.00	0.39	6
	Ψ (Bank_{Eroded}), \hat{p} (Gear, -Effort, -Velocity_{Mean})	*180.02	5.01	0.03	10
	+Section				
Adult-Juvenile	Ψ (-Proximity), \hat{p} (Gear, -Section)	*176.22	0.00	0.39	6
	Ψ (Bank_{Eroded}), \hat{p} (Gear, +Temp, -Effort, -Velocity_{Mean})	185.03	8.81	0.00	11
	+Section				
Autumn					
Adult-Juvenile	Ψ (Bank _{Eroded}), \hat{p} (Gear, -Proximity, -Section)	*248.56	0.00	0.98	9
	Ψ (Bank_{Eroded}), \hat{p} (Gear, -Effort, -Velocity_{Mean})	*261.23	12.67	0.00	10
	+Section				

Table 2.3. Estimated detection probabilities (\hat{p}) and standard error [in parenthesis; adjusted by the variance inflation factor (\hat{c})] for night electric fishing (EF), 6.4-mm mesh hoop net (HN_{6.4}), and 19-mm mesh hoop net (HN₁₉) for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013).

Season and life history stage	Detection probability (\hat{p})		
	EF	HN _{6.4}	HN ₁₉
Summer			
Adult	0.30 (0.20 – 0.41)	0.27 (0.18 – 0.39)	0.09 (0.05 – 0.18)
Juvenile	0.35 (0.26 – 0.46)	0.26 (0.17 – 0.36)	0.10 (0.05 – 0.17)
Adult-Juvenile	0.35 (0.26 – 0.46)	0.26 (0.17 – 0.36)	0.10 (0.05 – 0.17)
Autumn			
Adult-Juvenile	0.39 (0.28 – 0.52)	0.46 (0.33 – 0.59)	0.18 (0.10 – 0.30)

Table 2.4. Beta estimates from top models used to evaluate the occupancy (Ψ) and detection probability (\hat{p}) for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). Parameter estimates and confidence limits are presented on the odds-scale. Asterisks indicate significant parameter estimates.

Season and model	Covariates	Estimate	Confidence limits	
			Lower	Upper
Autumn				
Ψ (Bank _{Talus}), \hat{p} (Gear, Proximity, Section)				
	Ψ	1.75 ^{e+00}	5.70 ^{e-01}	5.39 ^{e+00}
	Ψ (Bank _{Talus})	1.24 ^{e+03}	1.63 ^{e-04}	9.44 ^{e+09}
	*p (Section)	1.14 ^{e-07}	9.65 ^{e-09}	1.34 ^{e-06}
	*HN _{6,4} (Proximity)	9.12 ^{e-02}	6.41 ^{e-02}	1.30 ^{e-01}
	*HN ₁₉ (Proximity)	1.12 ^{e-01}	7.65 ^{e-02}	1.65 ^{e-01}
	*EF (Proximity)	1.45 ^{e-01}	1.06 ^{e-01}	1.98 ^{e-01}
	*HN _{6,4}	8.69 ^{e+11}	1.49 ^{e+10}	5.06 ^{e+13}
	*HN ₁₉	4.05 ^{e+10}	5.56 ^{e+08}	2.95 ^{e+12}
	*EF	1.55 ^{e+10}	3.86 ^{e+08}	6.25 ^{e+11}

Appendix 2.1. Candidate models used to evaluate the influence of site- and sample-scale covariates on occupancy (Ψ) and detection probability (\hat{p}) for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). Akaike's Information Criterion (AIC_c) adjusted for small sample size or quasi-Akaike's Information Criterion (QAIC_c) adjusted for overdispersion was used to rank all candidate models. Models ranked using QAIC_c are indicated with an asterisk. Model weight (w_i), total number of parameters (K), and two times the log-likelihood ($-2\log(l)$) are also included.

Season	Life stage	Model	AIC _c or QAIC _c	Δ AIC _c or QAIC _c	w_i	K	$-2\log(l)$		
Summer	Adult	Ψ (Bank _{Eroded}), \hat{p} (Gear, Section)	*160.26	0.00	0.4508	6	283.02		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{Mean} , Section)	*162.72	2.46	0.1318	9	268.20		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Effort, Section)	*163.03	2.77	0.1129	7	282.35		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Temp, Section)	*163.36	3.10	0.0957	7	283.00		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Talus} , Section)	*164.35	4.09	0.0583	9	271.43		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{CV} , Section)	*166.11	5.85	0.0242	9	274.91		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{BP} , Section)	*166.48	6.22	0.0201	9	275.65		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Veg} , Section)	*166.56	6.30	0.0193	9	275.80		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Eroded} , Section)	*166.73	6.47	0.0177	9	276.15		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{AV} , Section)	*166.78	6.52	0.0173	9	276.24		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{CO-BP} , Section)	*167.39	7.13	0.0128	9	277.45		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Proximity, Section)	*167.85	7.59	0.0101	9	278.36		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Secchi, Section)	*168.26	8.00	0.0083	9	279.18		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{Mean} , Section)	*168.74	8.48	0.0065	9	280.12		
		Ψ (Bank_{Eroded}), \hat{p} (Gear, Temp, Effort, Velocity_{Mean}, Section)							
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Mp, Section)	*168.83	8.57	0.0062	11	264.84		
		Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{CV} , Section)	*169.68	9.42	0.0041	9	281.98		
			*169.75	9.49	0.0039	9	282.13		
		Juvenile		Ψ (Bank _{Eroded}), \hat{p} (Gear, Section)	*175.01	0.00	0.3883	6	312.72

Appendix 2.1. cont'd

Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{Mean} , Section)	*177.22	2.21	0.1286	9	297.37
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Talus} , Section)	*177.34	2.33	0.1211	9	297.62
Ψ (Bank _{Eroded}), \hat{p} (Gear, Temp, Section)	*177.87	2.86	0.0929	7	312.23
Ψ (Bank _{Eroded}), \hat{p} (Gear, Effort, Section)	*177.96	2.95	0.0888	7	312.40
Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{B1} , Section)	*178.65	3.64	0.0629	9	300.22
Ψ (Bank_{Eroded}), \hat{p} (Gear, Effort, Velocity_{Mean}, Section)	*180.02	5.01	0.0317	10	295.45
Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{CV} , Section)	*181.12	6.11	0.0183	9	305.12
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Veg} , Section)	*181.74	6.73	0.0134	9	306.34
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Eroded} , Section)	*182.04	7.03	0.0116	9	306.94
Ψ (Bank _{Eroded}), \hat{p} (Gear, Proximity, Section)	*182.42	7.41	0.0096	9	307.69
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{AV} , Section)	*183.02	8.01	0.0071	9	308.88
Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{CO-B1} , Section)	*183.09	8.08	0.0068	9	309.02
Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{Mean} , Section)	*183.29	8.28	0.0062	9	309.41
Ψ (Bank _{Eroded}), \hat{p} (Gear, Mp, Section)	*183.75	8.74	0.0049	9	310.33
Ψ (Bank _{Eroded}), \hat{p} (Gear, Secchi, Section)	*183.96	8.95	0.0044	9	310.74
Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{CV} , Section)	*184.49	9.48	0.0034	9	311.80
Adult- Juvenile					
Ψ (Bank _{Eroded}), \hat{p} (Gear, Section)	*176.22	0.00	0.3942	6	312.72
Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{Mean} , Section)	*178.36	2.14	0.1352	9	297.37
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Talus} , Section)	*178.49	2.27	0.1267	9	297.62
Ψ (Bank _{Eroded}), \hat{p} (Gear, Temp, Section)	*179.07	2.85	0.0948	7	312.23
Ψ (Bank _{Eroded}), \hat{p} (Gear, Effort, Section)	*179.16	2.94	0.0906	7	312.4
Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{B1} , Section)	*179.81	3.59	0.0655	9	300.22
Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{CV} , Section)	*182.30	6.08	0.0189	9	305.12
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Veg} , Section)	*182.91	6.69	0.0139	9	306.34
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Eroded} , Section)	*183.22	7.00	0.0119	9	306.94
Ψ (Bank _{Eroded}), \hat{p} (Gear, Proximity, Section)	*183.60	7.38	0.0098	9	307.69
Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{AV} , Section)	*184.20	7.98	0.0073	9	308.88
Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{CO-B1} , Section)	*184.28	8.06	0.007	9	309.02

Appendix 2.1. cont'd

	Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{Mean} , Section)	*184.47	8.25	0.0064	9	309.41
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Mp, Section)	*184.94	8.72	0.005	9	310.33
	Ψ (Bank_{Eroded}), \hat{p} (Gear, Temp, Effort, Velocity_{Mean}, Section)	185.03	8.81	0.0048	11	295.13
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Secchi, Section)	*185.15	8.93	0.0045	9	310.74
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{CV} , Section)	*185.69	9.47	0.0035	9	311.8
Autumn						
Adult-Juvenile	Ψ (Bank _{Eroded}), \hat{p} (Gear, Proximity, Section)	248.56	0.00	0.9827	9	220.56
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{Mean} , Section)	256.94	8.38	0.0149	9	228.94
	Ψ (Bank_{Eroded}), \hat{p} (Gear, Effort, Velocity_{Mean}, Section)	261.23	12.67	0.0017	10	228.29
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Section)	*265.50	16.94	0.0002	6	249.50
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Mp, Section)	*266.61	18.05	0.0001	9	238.61
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Secchi, Section)	*266.84	18.28	0.0001	7	247.24
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{BI} , Section)	*267.45	18.89	0.0001	9	239.45
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Temp, Section)	*268.23	19.67	0.0001	7	248.63
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Effort, Section)	*268.74	20.18	0.0000	7	249.14
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{AV} , Section)	*271.54	22.98	0.0000	9	243.54
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Velocity _{CV} , Section)	*272.70	24.14	0.0000	9	244.70
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Substrate _{CO-BI} , Section)	*272.72	24.16	0.0000	9	244.72
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{Mean} , Section)	*274.04	25.48	0.0000	9	246.04
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Veg} , Section)	*274.18	25.62	0.0000	9	246.18
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Depth _{CV} , Section)	*274.78	26.22	0.0000	9	246.78
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Talus} , Section)	*275.22	26.66	0.0000	9	247.22
	Ψ (Bank _{Eroded}), \hat{p} (Gear, Bank _{Eroded} , Section)	*275.81	27.25	0.0000	9	247.81

Appendix 2.2. Detection history for three sampling gears and three sampling occasions for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). For each gear, detection history is reported in order of sampling occasions 1, 2 and 3. Sampling gears were electric fishing (EF), small-mesh hoop nets (HN_{6,4}) and large-mesh hoop nets (HN₁₉). A 1 indicates a fish was detected at a site and a 0 indicates no fish were detected at that site.

Season	Life stage	Detection history			Times observed
		EF	HN _{6,4}	HN ₁₉	
Summer					
	Adult	000	000	000	16
		000	001	000	4
		001	000	000	4
		001	001	000	1
		000	010	000	1
		000	011	000	1
		000	001	010	1
		000	000	010	1
		000	001	010	1
		010	000	000	1
		011	010	010	1
		001	100	000	1
		011	111	001	1
		010	110	100	1
		100	001	000	1
		100	011	000	1
		110	000	000	1
		110	001	000	1
		100	110	000	1
		111	110	000	1
		100	001	111	1
	Juvenile	000	000	000	12
		000	001	000	4
		001	000	000	3
		001	000	001	1
		000	010	000	1
		000	011	000	3
		000	000	010	1
		000	001	010	1
		010	000	000	1
		011	010	010	1
		000	100	000	2
		001	100	000	1
		011	111	001	1
		010	111	100	1
		100	001	000	1
		100	011	000	2
		110	000	000	1
		110	001	000	1
		100	110	000	1
		111	110	000	1

Appendix 2.2. cont'd

	100	001	111	1
Adult-Juvenile	000	000	000	12
	000	001	000	4
	001	000	000	3
	001	000	001	1
	000	010	000	1
	000	011	000	2
	001	011	000	1
	000	000	010	1
	000	001	010	1
	010	000	000	1
	011	010	010	1
	000	100	000	2
	001	100	000	1
	011	111	001	1
	010	111	100	1
	100	001	000	1
	100	011	000	2
	110	000	000	1
	110	001	000	1
	100	110	000	1
	111	110	000	1
	100	001	111	1
Autumn				
Adult-Juvenile	000	000	000	8
	000	001	000	1
	000	000	001	1
	000	011	000	1
	000	011	001	1
	001	010	001	1
	010	000	000	1
	011	000	000	1
	001	100	000	1
	000	111	000	1
	010	100	000	1
	010	111	000	1
	100	000	000	1
	101	011	010	1
	111	000	010	1
	101	101	000	1
	101	100	010	1
	111	110	010	1
	111	000	100	2
	101	111	110	1

Chapter 3: Habitat Use of Non-Native Burbot in a Western River

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Abstract

Burbot *Lota lota* (Linnaeus) were illegally introduced into the Green River drainage, Wyoming in the 1990s. Burbot could potentially alter the food web in the Green River, thereby negatively influencing socially, economically, and ecologically important fish species. Therefore, managers of the Green River are interested in implementing a suppression program for Burbot. Because of the cost associated with the removal of undesirable species, it is critical that suppression programs are as effective as possible. Unfortunately, relatively little is known about the habitat use of non-native Burbot in lotic systems, severely limiting the effectiveness of any removal effort. We used hurdle models to identify habitat features influencing the presence and relative abundance of Burbot. A total of 260 Burbot was collected during 207 sampling events in the summer and autumn of 2013. Regardless of the season, large substrate (e.g., cobble, boulder) best predicted the presence and relative abundance of Burbot. In addition, our models indicated that the occurrence of Burbot was inversely related to mean current velocity. The efficient and effective removal of Burbot from the Green River largely relies on an improved understanding of the influence of habitat on their distribution and relative abundance.

Introduction

Freshwater ecosystems are among the most vulnerable systems to invasions by non-native species (Marchetti et al., 2004). A general decline in freshwater biodiversity and an increase in imperilment of native fishes can largely be attributed to the introduction of non-native fishes (Rahel, 2002). Non-native species negatively influence native species through a myriad of mechanisms, including predation (White & Harvey, 2001; Taniguchi et al., 2002;

McDowall, 2006), hybridization (Scribner et al., 2001; Allendorf et al., 2004; McDonald et al., 2008; Muhlfeld et al., 2009), competition (Mills et al., 2004; McHugh & Budy, 2005; McDowall, 2006), habitat modification (Pimentel et al., 2005; McDowall, 2006), and transmission of pathogens (Naylor et al., 2005; Gozlan et al., 2006). Negative effects on native species are often compounded because mechanisms are not independent of one another and often co-occur. For example, non-native common carp, *Cyprinus carpio* (Linnaeus), feed on both macroinvertebrates and macrophytes. As a result, the biomass of macroinvertebrates is reduced directly through predation and indirectly through a reduction in macrophytes which provide habitat for macroinvertebrates (Parkos III et al., 2003). While only about 1% of non-native species become established, their unknown effects on ecosystems and native species are a major concern for natural resource managers (Copp et al., 2005).

Methods to control the spread of non-native species can be categorized as preventative, early eradication, or prolonged suppression (Peterson & Paukert, 2009; Pyšek & Richardson, 2010). Preventative methods are ideal; however, non-native species are often discovered only after becoming established. Although established non-natives can sometimes be eradicated, successful eradication is often contingent on early detection which requires constant monitoring (Chornesky & Randall, 2003; Pyšek & Richardson, 2010). Monitoring for the presence of non-native species is generally difficult and is complicated by inadequate funding, logistic constraints, and identification of areas vulnerable to invasion (Chornesky & Randall, 2003; Pyšek & Richardson, 2010). For many non-native species, the only option is long-term suppression that attempts to maintain the species at low abundance to ameliorate their negative effects on ecosystems (Simberloff, 2003; Mueller, 2005).

Programs focused on eradication or suppression of non-native species are time consuming and costly; thus, designing efficient programs is critically important for natural resource agencies (Pimentel et al., 2005; Baxter et al., 2007; Berthou, 2007). Efficient suppression of non-native species generally requires basic knowledge of species occurrence. However, one of the primary challenges in any suppression effort is identifying the spatial and temporal distribution of a species. As such, natural resource scientists generally rely on habitat associations to predict species occurrence and distribution (Rieman & McIntyre, 1995; Rich et al., 2003; Sindt et al., 2012). Unfortunately, information on species-specific habitat use is often lacking, requiring further research into the relationship between habitat characteristics and species occurrence and relative abundance. Once basic information on species occurrence and relative abundance is understood, then undesirable species can be effectively and efficiently targeted for removal.

One such regionally undesirable, non-native species is Burbot, *Lota lota* (Linnaeus; Gardunio et al., 2011). Burbot are the only freshwater member of the family Gadidae (Howes, 1991). They have a circumpolar distribution that rarely extends south of 40°N, and occupy a diversity of lentic and lotic habitats throughout Europe, Asia, and North America (Tammi et al., 1999; McPhail & Paragamian, 2000; Stapanian et al., 2008 & 2010). In the 1990s, Burbot were illegally introduced into the Big Sandy River, Wyoming (Gardunio et al., 2011; Fig. 1). Since their introduction, Burbot have been sampled upstream of the confluence of the New Fork and Green rivers downstream to Dinosaur National Monument on the Utah-Colorado border (Gardunio et al., 2011). The presence of Burbot in the Green River system raises concern regarding management of socially and economically important trout fisheries (i.e., Brown Trout *Salmo trutta* Linnaeus, Rainbow Trout *Oncorhynchus mykiss* [Walbaum],

Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus* [Richardson]) and the conservation of native nongame fishes (i.e., Bluehead Sucker *Catostomus discobolus* Cope, Flannelmouth Sucker *Catostomus latipinnis* Baird & Girard, Roundtail Chub *Gila robusta* Baird & Girard; WGFD, 2010; Gardunio et al., 2011). Despite these concerns, the effective management of Burbot in the Green River has been stymied by insufficient information on their basic biology and ecology. To our knowledge, no studies have evaluated habitat use of non-native Burbot. The niche conservatism concept suggests that Burbot should maintain ecological requirements across different geographical distributions and time periods (Wiens & Graham, 2005; Wiens et al. 2010). However, due to limited occurrences of non-native Burbot, little evidence is available regarding habitat use of Burbot outside their native distribution. Without a clear understanding of the habitat used by non-native Burbot, efforts directed at their removal will be costly and largely ineffective. Therefore, the objectives of this study were to identify habitat characteristics that influence the occurrence and relative abundance of non-native Burbot in a Western lotic system and to evaluate the applicability of the niche conservatism concept.

Study Site

The Green River is the largest tributary of the Colorado River and drains portions of Wyoming, Utah, and Colorado (WGFD, 2010). The Green River originates in the Wind River Range of western Wyoming and flows for approximately 235 km before entering Fontenelle Reservoir. From Fontenelle Reservoir, the Green River flows for about 150 km until it enters Flaming Gorge Reservoir at the Wyoming-Utah border (Fig. 3.1; WGFD, 2010). Upstream of Fontenelle Reservoir, the Green River is characterized by high-gradient runs

interspersed with pool-riffle habitat and substrate characteristics of alluvial deposits (i.e., cobble, gravel, sand, and silt; Kurtz, 1980). From Fontenelle Dam to its confluence with the Big Sandy River, the Green River is characterized by moderate- to low-gradient runs averaging about 450 m in length (Wiley, 1974). From its confluence with the Big Sandy River, the Green River is relatively low-gradient with primarily sand and gravel substrate until entering Flaming Gorge Reservoir (Wiley, 1974). Most of the Green River basin is characteristic of a high desert climate with monthly temperature averages of -9°C (January) and 17°C (July) and low annual precipitation (25.4 cm; WGFD, 2010).

Methods

Sampling was conducted in four river sections during the summer (May 22 – July 12, 2013) and two river sections during autumn (September 6 – 25, 2013; Fig. 3.1). Sections were not a unit of interest; rather, they were simply used to allocate sampling effort. Each section was divided into 150-m long reaches. In total, 49 150-m long reaches were randomly selected for sampling ($n = 41$ in summer; $n = 28$ in autumn). Reaches were sampled with large-mesh hoop nets (19-mm bar mesh), small-mesh hoop nets (6.4-mm bar mesh), and night electrofishing. Each reach was sampled with a single gear per day. A sampling event was considered a consecutive three day period that consisted of sampling using a small-mesh hoop net, a large-mesh hoop net, and night electrofishing. Sampling events were replicated over a nine-day period such that each reach was sampled three times by each gear. Because the same amount of effort was used at each reach (i.e., all three gears), catch rates were calculated as the number of fish per sampling event (i.e., three day period). Due to logistic constraints associated with spring runoff, the summer sampling season commenced at the most

downstream section and continued upstream until all reaches were sampled. To increase sample size during autumn, 19 reaches were added to the 41 reaches sampled in the summer. However, due to unusually high precipitation and logistical constraints, only the most upstream reaches ($n = 15$; section 1, Fig. 3.1) and the reaches immediately downstream of Fontenelle Dam ($n = 13$; section 3) were sampled during autumn.

The small-mesh hoop nets had seven 0.6-m diameter hoops and an overall length of 3 m. In the event of a lost net, a fish “escape route” was placed between the sixth and seventh hoop. “Escape routes” consisted of a 20 cm \times 20 cm square opening covered with 6.4-mm bar measure mesh secured with 3-mm untreated cotton twine. In the event of a “lost” net, the cotton twine would deteriorate allowing entrained fish to escape. The large-mesh hoop nets had four 0.91-m diameter hoops and an overall length of 2.9 m. Each net had a “Mammalian Escape Hatch” placed between the third and fourth hoop, consisting of a 20 cm \times 41 cm square opening covered with a 36 cm \times 61 cm square section sewn on three sides. Each net was positioned parallel to the current with the cod end anchored upstream. Hoop nets were randomly assigned to each site on the first day of each sampling event. Existing hoop nets were removed the following day and replaced with the other size of hoop net. Nets were baited with white sucker, *Catostomus commersonii* (Lacépède), a non-native species in the system, and fished for approximately 24 hours. Effort was recorded as the total number of minutes each hoop net was in the water. Night electrofishing was conducted using a drift boat equipped with a 5,000 W generator and Smith-Root VVP-15B electrofisher (Smith-Root, Vancouver, WA). Electrofishing power output was standardized to 2,750 – 3,200 W (Miranda, 2009). One netter was positioned on the bow of the boat using a 2.4-m long dip net with 6-mm bar knotless mesh. Night electric fishing was conducted on the third day of each

sampling event to avoid biasing hoop net detections. Electrofishing proceeded downstream from the uppermost point of each 150 m reach. Fish were enumerated, weighed (g), and measured for total length (mm). All fish in this study were handled following the University of Idaho Institutional Animal Care and Use and American Veterinary Medical Association guidelines. Effort was recorded as the total number of seconds electricity was applied to the water.

Habitat variables (i.e., current velocity, depth, dominant substrate, in-stream cover, bank type) that were hypothesized to affect the occurrence and relative abundance of Burbot were measured once per season at each reach. Reaches with a single channel-unit type (i.e., riffle, run, pool) were divided in half by length and sampled separately for habitat characteristics. Channel units were sampled separately for habitat characteristics (i.e., depth, width, current velocity, dominant substrate, in-stream cover, bank type). Channel-unit length and width were measured to the nearest 0.5 m using a laser rangefinder. In-stream habitat characteristics were measured along a diagonal transect from the upper-most point of the channel unit to the lower-most point of the channel unit on the opposite bank. In-stream habitat characteristics (i.e., current velocity, dominant substrate, in-stream cover, depth) were measured at 20, 40, 50, 60, and 80% of transect width (Flotemersch et al., 2006; Sindt et al., 2012). Depth was measured to the nearest 0.1 m using a 2 m sounding pole or a handheld depth finder (Marcum LX-i, Minnetonka, Minnesota). Current velocity was measured to the nearest 0.01 m/s using a portable flowmeter (Flo-Mate Model 2000; Marsh-McBirney Inc, Loveland, CO). The dominant substrate was visually estimated as organic matter-silt (< 0.00 – 0.27 mm), sand and gravel (0.27 – 64.0 mm), cobble (64.0 – 260.0 mm), boulder (> 270.0 mm), or bedrock (modified from Orth & Maughan, 1982). Presence or absence of cover (i.e.,

large-woody debris, overhanging vegetation, undercut banks, boulders, macrophytes, anthropogenic structures) was recorded at each transect point (Fitzpatrick et al., 1998; Neebling & Quist, 2011). The proportion of each bank type (i.e., alluvium and vegetation, eroded, undercut, vegetation, boulder, anthropogenic structure, woody debris, sand and gravel) was estimated for each reach. An additional bank type called “alluvium bluff” was estimated for each reach and was characterized by steep, eroded banks with large substrate (≥ 64.0 mm; modified from Jaeger et al., 2005). In addition to reach-specific habitat variables, sample-specific habitat variables (i.e., Secchi disk depth [0.1 m], temperature [$^{\circ}$ C], conductivity [μ S/cm]) were measured at each sampling event following fish sampling.

A Spearman’s rank-order correlation coefficient ($|\rho|$) was used to assess correlation among covariates (Sindt et al., 2012). If two covariates were highly correlated ($|\rho| > 0.70$), only the most ecologically important and interpretable variable was used in candidate models (Burnham & Anderson, 2002). For example, mean depth was highly correlated with maximum depth ($|\rho| > 0.85$). However, mean depth was used because it better represented depth of the overall reach.

The relationship between habitat characteristics and Burbot occurrence and relative abundance was investigated using hurdle models. Hurdle models are two-stage regressions in which the first stage predicts the probability of a species’ presence at a reach using logistic regression (binomial distribution; Martin et al., 2005). The second stage is used to investigate the relationship between the relative abundance of Burbot and habitat characteristics using count data truncated at zero (i.e., count data > 0 ; Poisson distribution; Martin et al., 2005). Hurdle models are commonly used to deal with zero-inflated data in that zeros and non-zero counts can be modeled separately (Maunder & Punt, 2004; Garrido et al., 2009; Goetz et al.,

2012). Two-stage models also allow for the hypothesis that the factors driving presence and relative abundance are different (Wenger & Freeman, 2008).

Hurdle models were constructed using the GLM function in program R (R Development Core Team, 2013). Model fit was evaluated using the dispersion parameter of the most parameterized model from each stage. The dispersion parameter (\hat{c}) was calculated by dividing Pearson's residual deviance by the residual degrees of freedom (Burnham and Anderson, 2002). A \hat{c} greater than one indicated that the model either did not fit the data well or that the data were overdispersed; thus, model variance was adjusted using \hat{c} (Burnham & Anderson, 2002). In addition, model fit was assessed using McFadden's pseudo R^2 which is calculated as one minus the difference of the \log_e of the likelihood of the parameterized model and the \log_e of the likelihood of the intercept-only model (McFadden, 1974). McFadden's R^2 is commonly used to assess model fit with values of 0.20 – 0.40 representing excellent model fit; however, values as low as 0.10 have been shown to have good model fit (Hosmer & Lemshow, 1989). Therefore, models with a McFadden's $R^2 \geq 0.10$ were considered to have good model fit.

Eighteen candidate models from each modeling stage were ranked using Akaike's Information Criterion adjusted for small sample size (AIC_c ; Burnham & Anderson, 2002). Models with the lowest AIC_c value were considered the most supported models from each suite of candidate models. Overdispersed models were ranked using quasi- AIC_c ($QAIC_c$) and an additional parameter was added to further penalize overdispersed candidate models (Burnham & Anderson, 2002). All models with a ΔAIC_c or $\Delta QAIC_c$ of ≤ 2 were considered plausible (Burnham & Anderson, 2002; Schloesser et al., 2012).

Results

Habitat characteristics varied little among reaches within a section but were highly variable between river sections and season (Table 3.1). For example, the most downstream reaches averaged about 12% ($\sigma^2 = 3\%$) large substrate (cobble and boulder); whereas, reaches immediately downstream of Fontenelle Dam averaged approximately 83% (8%) large substrate. Similarly, an overall difference of 64% alluvium and vegetated bank was apparent between reaches directly upstream of Flaming Gorge Reservoir and those immediately downstream of Fontenelle Dam. Depth and current velocity were relatively homogenous throughout sections of the Green River. A difference of only 0.24 m in mean depth was observed during the summer between the shallowest (mean depth \pm SE; 0.89 ± 0.06 m) and deepest (1.13 ± 0.05 m) sections. Current velocity also exhibited low variability with a difference of 0.22 m/s among all river sections.

During the summer and autumn of 2013, 230 Burbot were caught during 95 of 207 sampling events. Night electrofishing sampled the most Burbot ($n = 116$), followed by small-mesh hoop nets ($n = 91$), with the remaining 23 fish caught with large-mesh hoop nets. An average of 0.022 Burbot were caught per sampling event (SE = 0.003). Due to the inherent difficulty in comparing catch rates between passive and active gears, gear efficiencies were evaluated using detectability in a separate study (Klein et al., *in review*). The mean length of Burbot sampled increased from the summer (mean length \pm SE; 333.4 ± 8.9 mm) to autumn (435.7 ± 10.4 mm).

The percentage of boulder substrate and mean current velocity best predicted the probability of occurrence of Burbot (Table 3.2). Burbot presence was positively related to boulder substrate and negatively related to mean current velocity. The relative abundance of

Burbot at a reach was positively correlated to alluvium bluff and negatively correlated with mean current velocity. The occurrence and relative abundance of Burbot was seasonally variable. The probability of Burbot being present at a site decreased during autumn.

However, the relative abundance sub-model indicated an overall increase in the relative abundance of Burbot during autumn compared to the summer.

Discussion

Regardless of the season, large substrate (i.e., alluvium bluff, boulder, cobble-boulder) was an important predictor of Burbot occurrence and relative abundance in the Green River, Wyoming. Among the existing studies investigating the relationship between Burbot occurrence and habitat, large substrate is often an important habitat characteristic (Edsall et al., 1993; Tzilkowski et al., 2004; Dixon & Vokoun, 2009). Dixon & Vokoun (2009) studied habitat selection of Burbot in Connecticut streams and concluded that substrate, substrate embededness, and depth were the primary habitat characteristics correlated with the presence of Burbot. More specifically, they reported that Burbot selected habitat with large substrate (i.e., boulders), low levels of substrate embededness, and deep water. Similarly, Eick (2013) reported that Burbot preferentially used habitat with large substrate (stone [63 – 200 mm]; cobble [> 200 mm]) in laboratory experiments. Previous research suggests that Burbot prefer large substrate over other types of cover. Dixon & Vokoun (2009) reported that Burbot disproportionally used large substrate in sites with large woody debris. A number of studies have concluded that the interstitial spaces between large substrate likely provide refugia for Burbot (McMahon et al., 1996; Fischer, 2000). Hofmann & Fischer (2002) posited that juvenile Burbot shelter in the interstitial spaces between substrate in littoral zones of lakes to

avoid predators. Adult Burbot, largely released from predation, likely use large substrate as a refuge from high current velocity (Fischer, 2000). Regardless of the exact mechanisms driving Burbot to select habitat with large substrate, it is clearly an important habitat characteristic selected by juvenile and adult Burbot.

In addition to a positive correlation with large substrate, each model showed a negative relationship between mean current velocity and Burbot occurrence and relative abundance. Smith (2013) reported an inverse relationship between juvenile Burbot occupancy and mean current velocity near the substrate in western U.S. lotic systems. Similarly, Dillen et al. (2008) found that juvenile Burbot selected habitat with low to moderate current velocities (i.e., 0.05 – 0.15 m/s) in lowland rivers in northeastern France. In the Alleghany River basin, Pennsylvania, Burbot were most commonly found in habitats with low current velocity (≤ 0.1 m/s; Fischer, 2008). In laboratory experiments, Jones et al. (1974) reported Burbot had poor swimming endurance in that they could not maintain their position for longer than 10 minutes at a current velocity of 25 cm/s. Similarly, Paragamian (2000) reported that the upstream movement of pre-spawn adult Burbot in the Kootenai River, Idaho was disrupted by increased discharge from Libby Dam, Montana. Thus, Burbot likely select habitats with relatively low mean current velocity because of their poor swimming endurance.

Depth is commonly cited as being a highly influential variable for predicting the presence of Burbot (Dillen et al., 2008; Dixon & Vokoun, 2009; Eick, 2013). However, none of our top models reflected the influence of depth on either Burbot occurrence or relative abundance. In laboratory experiments, Eick (2013) reported that Burbot selected habitats with greater depth. However, the maximum depth used in Eick's experiments was 90 cm making inference to natural systems tenuous. Similarly, Fischer (2008) reported that Burbot

occurred at higher frequencies in depths between 65 and 80 cm in the Alleghany River drainage, Pennsylvania. However, none of the reaches sampled by Fischer (2008) exceeded 80 cm in depth. Burbot may select habitats with deep water; however, it is unclear if Burbot preferentially select habitats for water depth or other habitat characteristics. For example, Slavík et al. (2005) reported that Burbot inhabited relatively shallow habitat with large substrate during daylight hours in the Ohře River, Czech Republic. Similarly, Dixon & Vokoun (2009) reported that depth was an important habitat characteristic in determining Burbot presence, but that the importance of depth was conditional on substrate type and substrate embededness. Therefore, it appears that large substrate is the primary feature influencing habitat selection of Burbot in lotic systems with the importance of water depth increasing as available cover decreases.

Niche conservatism is defined as the retention of niche-related ecological traits over time (Wiens et al., 2010). Although the concept is often discussed within the context of time, the concept can be extended to consider the retention of ecological traits across space, particularly as it relates to the translocation of a species. Our results support the niche conservatism concept in that native and non-native Burbot maintain ecological traits with regard to habitat use. A logical question is then why are Burbot in the Green River thriving while Burbot in similar lotic systems are declining? Population declines of native Burbot can be attributed to direct (e.g., harvest) and indirect (e.g., habitat alterations) anthropogenic influences. For instance, exploitation has been cited as being a primary cause of population declines of Burbot in the Wind-Bighorn River, Wyoming and the Kootenai River, Idaho (Hubert et al., 2008; Paragamian, 2000). Additionally, both the Wind-Bighorn and Kootenai rivers have experienced substantial water development in the last 100 years (Hubert et al.,

2008; Paragamian, 2000). In the Kootenai River, alterations to the natural flow regime during spawning migrations have been suggested to reduce fitness and stamina, influence vitellogenin synthesis, and disrupt synchrony in Burbot spawning (Paragamian, 2000). Entrainment of Burbot in irrigation canals has been posited as a major cause of mortality of Burbot in the Wind-Bighorn River (Hubert et al., 2008). Burbot in the Green River are rarely exploited and do not appear to be negatively influenced by operation of Fontenelle Dam. However, Burbot in the Green River are relatively new to the system and could simply be benefiting from an abundance of under-used resources. Without additional research ascertaining the mechanisms behind the proliferation of Burbot in the Green River will be difficult. Nevertheless, understanding the retention of ecological traits provides a context for guiding conservation and management actions for Burbot throughout their distribution.

The eradication of Burbot from the Green River is unlikely given their prevalence throughout much of the river upstream of Flaming Gorge Reservoir (Gardunio et al., 2011). As a result, management actions will likely focus on decreasing the abundance of Burbot in the Green River. Therefore, the efficient and effective removal of Burbot relies on basic information on the relationship between habitat characteristics and their distribution and relative abundance. Suppression programs often use information on the ecology of a species to enhance removal efforts. For example, Dux et al. (2011) used knowledge of lake trout, *Salvelinus namaycush* (Walbaum), distribution in Lake McDonald, Montana to refine suppression efforts and guide managers to more efficient removal efforts. Similarly, Penne & Pierce (2008) used associations between habitat characteristics and aggregations of common carp in Clear Lake, Iowa to inform more efficient removal efforts. Because the Green River harbors three fishes of conservation concern and economically important trout fisheries, the

suppression of Burbot in the Green River will likely rely on physical removal (e.g., hoop nets, electrofishing) rather than piscicides (e.g., rotenone) or biocontrols (e.g., predators, parasites). Physical removal of a species attempts to reduce the total abundance, and thus, the recruitment of a species within a system. Suppression of non-native species is fairly common (Neilson et al., 2004; Knapp et al., 2007); however, maintaining a species at low abundance requires consistent removal efforts that can be prohibitively expensive (Quist & Hubert, 2004; Baxter et al, 2007; Gozlan et al., 2010). Therefore, if non-native species are suppressed using physical removal, any effort to increase the efficiency of removal is advisable. By identifying areas with large substrate and relatively low current velocity, managers can more effectively target Burbot for removal in the Green River, Wyoming.

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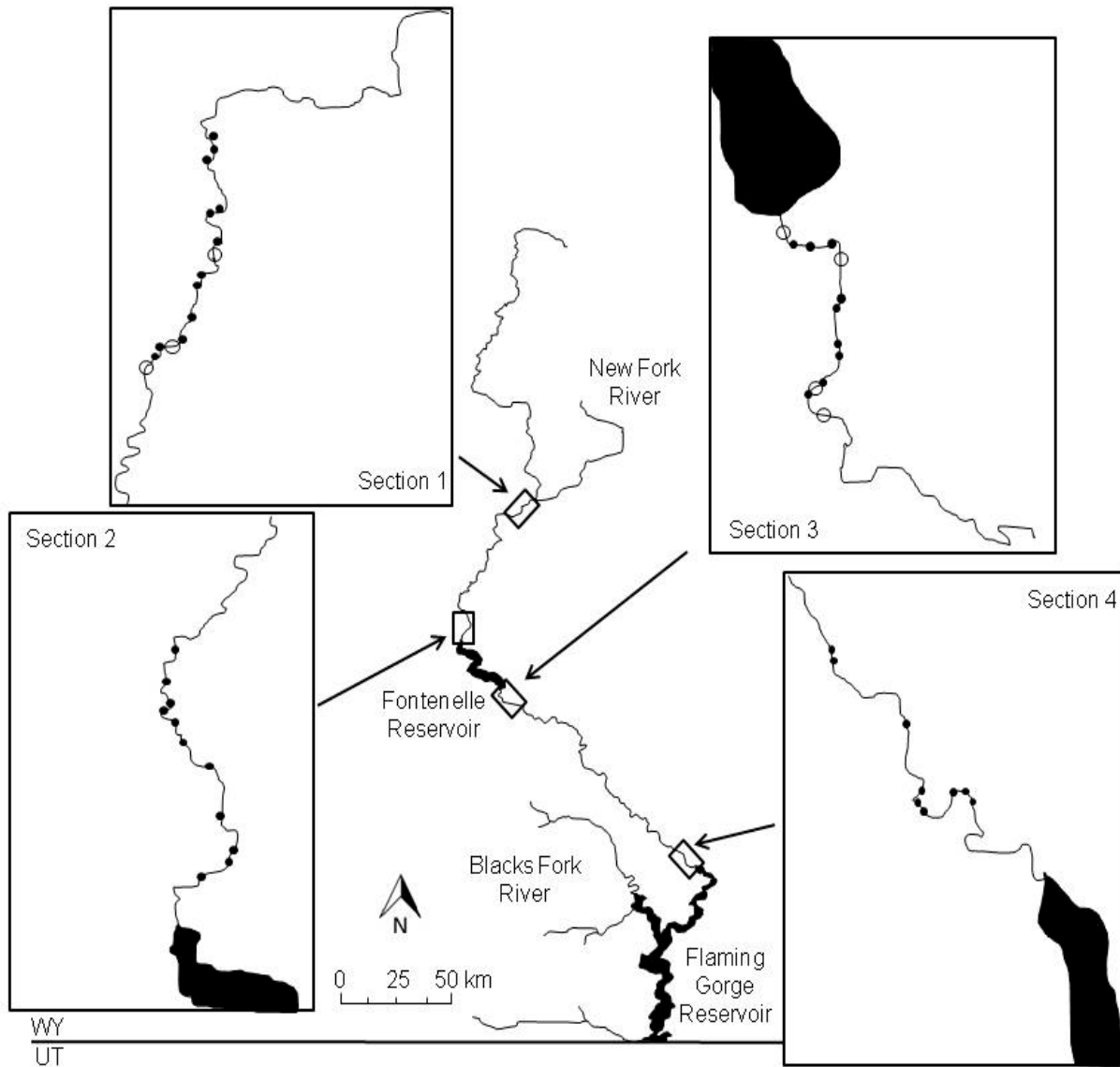


Figure 3.1. Sections used for Burbot sampling in the Green River, Wyoming during the summer and autumn (2013). Boxes depict each section in detail, with sites sampled in the summer (solid black circles) and sample sites added in autumn to increase sample size (open black circles).

Table 3.1. Mean and standard error (in parenthesis) of habitat characteristics used to evaluate occurrence and relative abundance of juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). River section 1 is the most upstream section followed by sections 2, 3, and 4.

Variable	Description	Season and section					
		Summer			Autumn		
		Section 1	Section 2	Section 3	Section 4	Section 1	Section 3
Depth _{CV}	Mean coefficient of variation of depth	0.36 (0.02)	0.38 (0.02)	0.31 (0.02)	0.34 (0.04)	0.31 (0.02)	0.30 (0.02)
Depth _{Mean}	Mean depth (m)	1.13 (0.05)	0.94 (0.02)	0.93 (0.03)	0.96 (0.10)	0.89 (0.06)	1.01 (0.06)
Velocity _{Mean}	Mean water column velocity (m/s)	0.60 (0.03)	0.55 (0.05)	0.61 (0.09)	0.39 (0.05)	0.40 (0.04)	0.45 (0.04)
Proximity	Distance from downstream reservoir (rkm)	46.86 (1.20)	8.77 (1.71)	120.70 (0.58)	8.72 (1.23)	46.28 (1.04)	120.60 (0.58)
Temp	Water temperature (°C)	19.94 (0.16)	18.80 (0.11)	14.65 (0.09)	16.07 (0.24)	16.19 (0.17)	17.10 (0.12)
Substrate _{Co-BI}	Percentage of cobble and boulder substrate (%)	0.53 (0.10)	0.81 (0.08)	0.83 (0.09)	0.12 (0.06)	0.63 (0.06)	0.93 (0.06)
Substrate _{BI}	Percentage of boulder substrate (%)	0.08 (0.04)	0.01 (0.01)	0.06 (0.06)	0.02 (0.02)	0.07 (0.03)	0.21 (0.03)
Bank _{Veg}	Percentage of vegetated bank (%)	0.51 (0.07)	0.50 (0.08)	0.07 (0.04)	0.41 (0.12)	0.42 (0.06)	0.16 (0.06)
Bank _{Av}	Percentage of alluvium - vegetated bank (%)	0.03 (0.02)	0.13 (0.05)	0.64 (0.10)	0.00 (0)	0.19 (0.06)	0.48 (0.06)
Bank _{Bluff}	Percentage of alluvium bluff bank (%)	0.14 (0.06)	0.14 (0.07)	0.15 (0.07)	0.29 (0.08)	0.17 (0.06)	0.22 (0.06)
Bank _{Eroded}	Percentage of eroded bank (%)	0.40 (0.05)	0.33 (0.05)	0.31 (0.09)	0.48 (0.09)	0.37 (0.07)	0.33 (0.07)
Mp	Percentage of instream macrophyte cover (%)	0.36 (0.09)	0.85 (0.07)	0.63 (0.13)	0.72 (0.11)	0.30 (0.04)	0.57 (0.04)
Effort	Total number of hours for each sampling event (hr)	43.50 (0.20)	45.33 (0.26)	44.08 (0.16)	46.68 (0.53)	46.45 (0.16)	47.88 (0.08)

Table 3.2. Candidate models used to evaluate the influence of covariates on the occurrence and relative abundance for juvenile and adult Burbot sampled in the Green River, Wyoming during the summer and autumn (2013). Akaike's Information Criterion (AIC_c) adjusted for small sample size or quasi-Akaike's Information Criterion ($QAIC_c$) adjusted for overdispersion was used to rank all candidate models. Model weight (w_i), total number of parameters (K), two times the log-likelihood ($-2\log(L)$), and McFadden's pseudo R^2 (R^2) are also included. The relationship between covariates and occurrence and relative abundance are indicated as positive (+) or negative (-). Only models with $a\Delta AIC < 2$ and the most parameterized model (italics) in each candidate set are included.

Sub-model	Model name	AIC_c or $QAIC_c$	ΔAIC_c or $\Delta QAIC_c$	w_i	K	$-2\log(L)$	R^2
Presence - Absence	+ Substrate _{Bl} , - Velocity _{Mean} , - Season	236.09	0.00	0.68	6	111.84	0.11
	+ <i>Depth_{CV}</i> , + <i>Depth_{Mean}</i> - <i>Velocity_{Mean}</i> - <i>Proximity</i> , + <i>Temp</i> , + <i>Substrate_{Co-Bl}</i> + <i>Substrate_{Bl}</i> - <i>Bank_{Veg}</i> - <i>Bank_{AV}</i> + <i>Bank_{Bluff}</i> - <i>Bank_{Eroded}</i> - <i>Mp</i> , + <i>Season</i>	238.88	2.79	0.17	28	86.88	0.31
Relative abundance	+ Bank _{Bluff} , - Velocity _{Mean} , + Season	285.46	0.00	0.50	6	136.14	0.08
	+ Bank _{Bluff} , + Season	287.21	1.75	0.21	4	139.33	0.06
		339.66	54.20	0.00	28	125.26	0.15

Chapter 4: Population Characteristics and the Suppression of Non-Native Burbot

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Management

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Abstract

Burbot *Lota lota* were illegally introduced in the Green River drainage, Wyoming and have since proliferated throughout the system. Burbot in the Green River pose a threat to native species and socially, economically, and ecologically important recreational fisheries. Therefore, managers of the Green River are interested in implementing a suppression program for Burbot. We collected demographic data on Burbot in the Green River and used the information to construct an age-based population model (female-based Leslie matrix) to evaluate the population-level response of Burbot to various management scenarios. Burbot in the Green River grew faster, matured at younger ages, and were more fecund than other Burbot populations within the species' native distribution. The age-structured population model, in conjunction with demographic information, indicated that the Burbot population in the Green River was not resource limited and could be expected to increase under current conditions. The model also indicated that the Burbot population in the Green River would decline once total annual mortality reached 58%. Population growth of Burbot in the Green River was most sensitive to age-0 and age-1 mortality. The age-structured population model indicated that by targeting younger age classes or increasing mortality of age-3 and older Burbot, the Burbot population can be effectively suppressed in the Green River, Wyoming.

Introduction

Freshwater ecosystems are among the most vulnerable systems to invasions by non-native species (Moyle 1999). A general decline in freshwater biodiversity and an increase in imperilment of native fishes can, in part, be attributed to the introduction of non-native fishes (Rahel 2002). Despite increasing evidence that non-native species have detrimental effects on

native fishes (Gozlan 2008; McDowall 2006), human activity continues to promote the spread of non-native fishes worldwide. For example, Copp et al. (2005) reported that 185 non-native freshwater fishes have been introduced to the United States alone. Although the spread of non-native fishes is primarily due to aquaculture (51% of non-native introductions) and the ornamental fish trade (21%), intentional (legal or illegal) introductions for commercial and recreational fisheries account for approximately 19% of non-native fish introductions worldwide (Gozlan 2008).

In the United States, there is a long history of intentional fish introduction (Rahel 2004). During the latter part of the 19th century, many states developed fish commissions whose primary task was to propagate fish species for recreational and commercial uses. For instance, the territory of Wyoming established a Board of Fish Commission in 1882, the mission of which was to “procure and distribute fish to public waters” with the intent of promoting “the increase and preservation of food fish” (Barkwell 1883). Many states had similar motivations, which led to the unrestrained introduction of fishes throughout the United States. Although the widespread introduction of sport fishes was once common, natural resource management agencies now realize the potential negative consequences of non-native fish introductions. For example, Lake Trout *Salvelinus namaycush* have been shown to negatively affect native salmonid populations in ecosystems where they have been successfully introduced (Fredenberg 2002; Vander Zanden et al. 2003; Martinez et al. 2009). Although it is increasingly uncommon for natural resource management agencies to introduce non-native fishes, unauthorized introductions continue to occur (Rahel 2004).

Unauthorized fish introductions are relatively common and act to offset the management efforts of natural resource agencies. For example, numerous introductions of

Walleye *Sander vitreus* and Northern Pike *Esox lucius* in the Pacific Northwest have negatively influenced salmonid populations through predation and competition for resources (McMahon and Bennet 1996). Although fish introductions occur through various mechanisms (e.g., bait-bucket release, escapes from aquaculture; Benson 1999; Litvak and Mandrak 1999), the illegal introduction of fish by anglers is perhaps the most widespread source of non-native fishes in the western United States. Rahel (2004) reported that 17 of the documented 31 species illegally introduced to Wyoming waters were sport fish. In the upper Colorado basin, illegal introductions by anglers have established 46 non-native fish populations in at least 22 reservoirs (Johnson et al. 2009). In Maine, the establishment of populations of Northern Pike, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *M. dolomieu*, Black Crappie *Pomoxis nigromaculatus*, Bluegill *Lepomis macrochirus*, and Green Sunfish *L. cyanellus* in over 150 lakes is the result of illegal introductions (Boucher 2007). Regardless of the mechanism and intent of a given fish introduction, the spread of non-native fishes throughout the United States continues to be a major problem for natural resource management agencies.

One example of an illegally introduced fish species is Burbot *Lota lota* in the Green River drainage of Wyoming. In the 1990s, Burbot were illegally introduced into Big Sandy Reservoir, Wyoming. Following their introduction, Burbot became established in Big Sandy Reservoir and began dispersing downstream into the Green River, Wyoming (Gardunio et al. 2011). Although the introduction of Burbot into Big Sandy Reservoir was likely the initial introduction of the species into the Green River drainage, there have likely been numerous introductions into different portions of the system over the years. For example, Burbot have been sampled upstream of Fontenelle Dam which acts as a barrier to upstream movement of

fish from Big Sandy Reservoir. Regardless of the number of introductions, Burbot are well established in the Green River drainage and represent a major concern for natural resource management agencies in Wyoming.

Burbot is the only freshwater member of the family Gadidae (Howes 1991). It has a circumpolar distribution that rarely extends below 40°N and occupies a diversity of lentic and lotic habitats throughout Eurasia and North America (McPhail and Paragamian 2000). Burbot are highly fecund with estimates varying from 6,300 (Miller 1970) to 3,477,699 eggs per female (Roach and Evenson 1993). Burbot are generally categorized as piscivores, with some authors estimating over 80% of the species diet consisting of fishes (McPhail and Paragamian 2000). However, recent research suggests that Burbot have fairly plastic diets as adults (Paragamian 2009; Gardunio et al. 2011). Gardunio et al. (2011) estimated that crayfishes *Astacoidea* spp. accounted for 75% of the diet of Burbot in Flaming Gorge Reservoir, Wyoming-Utah. Regardless of their specific diet, Burbot have the potential to alter the food web of the Green River through direct predation and interspecific competition. The widespread proliferation of Burbot throughout the Green River drainage raises concerns regarding management of socially and economically important recreational fisheries (e.g., Brown Trout *Salmo trutta*, Smallmouth Bass). In addition, the presence of Burbot in the Green River is troubling with regards to the conservation of native fishes (i.e., Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus*, Bluehead Sucker *Catostomus discobolus*, Flannelmouth Sucker *Catostomus latipinnis*, Roundtail Chub *Gila robusta*). To counteract the potential negative effects of Burbot, the Wyoming Game and Fish Department (WGFD) is interested in controlling the distribution and abundance of Burbot in the Green River drainage.

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

Methods

The Green River is the largest tributary of the Colorado River and drains approximately 124,578 km² in portions of Wyoming, Utah, and Colorado (Figure 4.1;

Wyoming Game and Fish Department 2010). The Green River originates in the Wind River Range of western Wyoming and flows for approximately 235 km before entering Fontenelle Reservoir. From Fontenelle Reservoir, the Green River flows for 150 km until entering Flaming Gorge Reservoir at the Wyoming-Utah border. From Utah, the river flows through portions of Colorado before returning to Utah where it joins the Colorado River. Major tributaries to the Wyoming portion of the Green River include the New Fork, East Fork, Big Sandy, Little Sandy, Hams Fork, Little Snake, Blacks Fork, and Henry's Fork rivers (Wyoming Game and Fish Department 2010). Twelve species and subspecies of fishes are native to the Green River; however, the Colorado Pikeminnow *Ptychocheilus lucius*, Bonytail *Gila elegans*, and Razorback Sucker *Xyrauchen texanus* have been extirpated from Wyoming (Wyoming Game and Fish Department 2010). The Green River is also home to five species of conservation concern (i.e., Bluehead Sucker, Flannelmouth Sucker, Roundtail Chub, Colorado River Cutthroat Trout, and Mountain Whitefish *Prosopium williamsoni*). In addition to Burbot, 28 non-native fishes have been introduced to the Green River drainage (Bezzarides and Bestgen 2002; Wyoming Game and Fish Department 2010). Most of the Green River basin is characteristic of a high desert climate with mean monthly temperatures of -9°C (January) and 17°C (July), and low annual precipitation (25.4 cm; Wyoming Game and Fish Department 2010). Vegetation of the Green River basin is predominantly sagebrush *Artemisia* spp. (sagebrush shrublands [53%], desert shrubland [21%], foothill shrubland [6%]). Land use in the Green River basin is dominated by energy development (i.e., natural gas, oil, coal, uranium), but also supports recreation and water development.

Sampling was conducted in four river sections (two upstream of Fontenelle Dam; two downstream of Fontenelle Dam; Figure 4.1) during the summer (May 22–July 12, 2013) and

two river sections (one upstream of Fontenelle Dam; one downstream of Fontenelle Dam) during autumn (September 6–25, 2013). Sections were not a unit of interest; rather, they were simply used to allocate sampling effort. Each section was divided into 150-m long reaches. In total, 49 150-m long reaches were randomly selected for sampling ($n = 41$ in summer; $n = 28$ in autumn). Reaches were sampled with large-mesh hoop nets (19-mm bar mesh), small-mesh hoop nets (6.4-mm bar mesh), and night electrofishing. Each reach was sampled with a single gear per day. A sampling event was considered a consecutive three-day period that consisted of sampling with a small-mesh hoop net, a large-mesh hoop net, and night electrofishing. Sampling events were replicated over a nine-day period such that each reach was sampled three times with each gear. Because the same amount of effort was used at each reach across all three gears, catch rates were calculated as the number of fish per sampling event (i.e., three-day period). Due to logistic constraints associated with spring runoff, the summer sampling season commenced at the most downstream section and continued upstream until all reaches were sampled. During the fall, 19 reaches were added to the 41 reaches sampled in the summer to increase sample size. However, because of unusually high precipitation and logistical constraints, only the most upstream reaches ($n = 15$; Section 1, Figure 4.1) and the reaches immediately downstream of Fontenelle Dam ($n = 13$; Section 3) were sampled during autumn.

Small-mesh hoop nets had seven 0.6-m diameter hoops and an overall length of 3 m. In the event of a lost net, a fish “escape route” was placed between the sixth and seventh hoop. “Escape routes” consisted of a 20 cm \times 20 cm square opening covered with 6.4-mm bar measure mesh secured with 3-mm untreated cotton twine. In the event of a “lost” net, the cotton twine would deteriorate allowing fish to escape. The large-mesh hoop nets had four

0.91-m diameter hoops and an overall length of 2.9 m. Each net had a “Mammalian Escape Hatch” placed between the third and fourth hoop, consisting of a 20 cm × 41 cm opening covered with a 36 cm × 61 cm section sewn on three sides. Each net was positioned parallel to the current with the cod end anchored upstream. Hoop nets were randomly assigned to each reach on the first day of each sampling event. Existing hoop nets were removed the following day and replaced with the other size of hoop net. Nets were baited with White Sucker *Catostomus commersonii*, a non-native species in the system, and fished for approximately 12 hours. Night electrofishing was conducted on the third day of each sampling event using a drift boat equipped with a 5,000 W generator and Smith-Root VVP-15B electrofisher (Smith-Root, Inc., Vancouver, Washington). Electrofishing power output was standardized to 2,750–3,200 W (Miranda 2009). One netter was positioned on the bow of the boat using a 2.4-m long dip net with 6-mm bar knotless mesh. Electrofishing proceeded downstream from the uppermost point of each 150 m reach. Effort was recorded as the total number of seconds that electricity was applied to the water.

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

Sagittal otoliths were used to estimate the age and growth of Burbot (Klein et al. *in press*). Otoliths were mounted in epoxy in 2.0 ml centrifuge tubes and transversely sectioned

about the nucleus (Edwards et al. 2011). Otolith cross-sections were approximately 0.5 mm thick. Cross-sections were examined using a dissecting microscope with transmitted light and an image analysis system (Image-Pro Plus; Media Cybernetics, Silver Springs, Maryland). Annuli were enumerated independently by two readers without knowledge of fish length and sampling location. Both readers had experience enumerating annuli of various structures prior to the study. After each reader assigned an age, age estimates were compared. If discrepancies existed between age estimates, the structure was re-aged by both readers and discussed in a mutual reading. If a consensus age could not be reached, the structure was removed from further analysis. An age-length key was used to apply the age and length distribution of subsampled Burbot ($n = 234$) to represent the age and length distribution for all Burbot sampled during the summer and autumn (Isely and Grabowski 2007; Quist et al. 2012).

Growth of Burbot was assessed using a von Bertalanffy growth model (VBM; Haddon 2001). Using the fisheries stock assessment (FSA) package in R (R Core Development Team 2014), a non-linear function was fit to length-at-age data of Burbot ($n = 234$) with 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 (Isely and Grabowski 2007; Quist et al. 2012).

Body condition of Burbot sampled from the upper and lower Green River was evaluated using relative weight (W_r ; Fisher et al. 1996; Neumann et al. 2012). Relative weight was calculated as the weight of an individual fish (W) divided by the standard weight of Burbot (W_s) multiplied by 100. Relative weight was evaluated by standard length categories for Burbot. Standard length categories include stock (≥ 200 mm), quality (≥ 380 mm), preferred (≥ 530 mm), memorable (≥ 670 mm), and trophy (≥ 820 mm; Neumann et al. 2012). Relative weight was calculated separately for fish sampled during the summer and autumn to account for seasonal variation in body condition.

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

Fecundity of up to five sexually mature female Burbot per 50-mm length category was estimated gravimetrically ($n = 45$; Murua et al. 2003). Both ovaries of an individual fish were blotted dry, weighed to the nearest 0.001 g, and one ovary was randomly selected for fecundity analysis. A subsample was removed from the posterior, medial, and anterior section of each ovary, weighed to the nearest 0.001 g, and eggs were enumerated (Murua et al. 2003). The number of eggs in each subsample was divided by the weight of the subsample to estimate the average number of eggs per gram. The number of eggs per gram of each

subsample was averaged and multiplied by the total ovary weight to estimate the total number of eggs per ovary (Murua et al. 2003). Mean fecundity at age (f_i) was calculated by age class for age-3 and older female Burbot. Linear regression was used to estimate the fecundity-length relationship of female Burbot.

The instantaneous total mortality rate (Z) of age-3 to age-9 Burbot was estimated from catch data using the Chapman-Robson estimator and the peak criterion (Chapman and Robson 1960; Smith et al. 2012). No estimate of Z was available for age-0 Burbot in natural systems; therefore, two estimates of Z were used in an attempt to “bracket” the instantaneous mortality rate of age-0 Burbot in the Green River (Worthington et al. 2011; Table 4.1). The “high” estimate of Z was calculated as the mean survival rate of eight groups of hatchery-produced Burbot stocked into earthen ponds for nine months (Vught et al. 2008). The “low” estimate of Z was obtained from a study where two groups of Burbot were stocked into earthen ponds and subjected to predation (Paragamian and Laude 2009).

Estimates of mortality for age-1 and age-2 Burbot were not available. Mortality is generally assumed to be highest in larval stages and decreases with fish age (and size; Houde 1997; Jennings et al. 2001). Therefore, Z was estimated for age-2 Burbot as the average of age-0 and age-3 Burbot assuming “high” and “low” age-0 mortality rates. Age-1 Burbot mortality was then estimated as the average of age-0 and age-2 Burbot assuming “high” and “low” age-0 mortality rates. Although estimated values of Z for either age-0 or age-3 and older Burbot could have been applied to age-1 and age-2 Burbot (i.e., a fixed value of Z), these estimates were likely unrealistic for age-1 and age-2 Burbot considering the generally assumed decrease in mortality with fish age (Jennings et al. 2001). All estimates of Z were assumed to be equal to the instantaneous natural mortality rate (M) because of limited angler

exploitation of Burbot in the Green River (D. Rhea, unpublished data). Instantaneous fishing mortality (F) was incorporated into population models to evaluate different management scenarios. Instantaneous fishing mortality was allowed to vary from 0–1.5 in increments of 0.1. Age-specific estimates of Z were converted to annual survival rate (S) as the relationship $S = e^{-Z}$ where $Z = F + M$ (Miranda and Bettoli 2007). Age-specific estimates of S were used for population modeling.

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

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

where Fert_1 – Fert_9 are fertility rates for age-0 through age-9 Burbot and S_1 – S_8 are the age-specific annual survival rate of Burbot at age t . Fertility rates (Fert_t) for each age t were calculated as:

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

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

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

Population growth (λ) was modeled under three management scenarios assuming “high” and “low” estimates of juvenile survival (i.e., S_0 , S_1 , S_2). Management scenarios assumed fishing mortality (F) was fully selected for age-1 and older Burbot, age-2 and older Burbot, and age-3 and older Burbot. Each management scenario was maintained for 10 years. Matrix models were not sensitive to starting population size because they did not incorporate density dependence. An estimate of total abundance (N) was unavailable for the Burbot population in the Green River; thus, an arbitrary value of 40,000 individuals was used for modeling. Because the observed sex ratio was 1:1, abundance estimates were multiplied by 0.5 for a total of 20,000 female Burbot. Each management scenario was simulated 1,000 times using functions from the “popbio” package in R (Stubben and Milligan 2007; R Core Development Team 2014). For each simulation, the population growth rate was computed as $\lambda_t = N_t / N_{t-1}$ over 10 year-long time steps and the mean λ_t was calculated over all time steps. The geometric mean of λ_t (λ_G ; $\pm 95\%$ CI) was then calculated to represent the average

population growth rate over 10 years (Morris and Doak 2002). The population was assumed to be declining from recruitment overfishing when λ_G was less than one (Haddon 2001).

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

Results

In total, 568 Burbot (235 lower Green River; 333 upper Green River) were sampled during the summer and autumn. Burbot in the lower Green River varied in length from 116 mm to 719 mm; whereas, Burbot sampled from the upper Green River varied in length from 52 mm to 606 mm (Figure 4.2). Burbot from the lower Green River varied in age from 0–9 and Burbot in the upper Green River varied in age from 0–7. Overall, Burbot in the Green River grew quickly and obtained high maximum lengths (Figure 4.3). Burbot varied in length from 52–719 mm with a mean length of 369 mm.

Mean W_r for stock-, quality-, and preferred-length Burbot was similar between the lower and upper Green River (Figure 4.4). Burbot greater than 670 mm (memorable length) were only present in the lower Green River during autumn and had a mean W_r of 88. Additionally, a general increase in W_r was observed from summer to autumn, but the seasonal difference in W_r was minimal.

Female Burbot in the Green River matured at an older age and at larger sizes than male Burbot. Female Burbot were first mature at age 3 which corresponded to a mean length of 341 mm. About 50% of the age-3 and all of the age-8 female Burbot were sexually mature (Table 4.1). Of the male Burbot sampled, males were first mature at age 2 which corresponded to a mean length of 273 mm. Approximately 50% of age-2 and all of the age-8 male Burbot were sexually mature.

Fecundity increased with age for all age classes (Figure 4.5). Age-3 female Burbot had a mean fecundity of 217,799 eggs ($\pm 25,033$). Age-6 female Burbot had a mean fecundity of 823,591 eggs ($\pm 49,884$) and age-9 female Burbot had a mean fecundity of 1,429,382 eggs ($\pm 108,720$).

Assuming low juvenile survival and no fishing mortality, the 10-year estimate of λ_G of Burbot in the Green River was 1.11 (95% CI = 1.09–1.12; Figure 4.6). When age-1 and older Burbot were targeted for removal, the population decreased below replacement when $F = 0.12$. An $F = 0.12$ corresponded to a mean total annual mortality rate (A) of 0.62 for age-1 and older Burbot. When age-2 and older Burbot were suppressed, the population decreased below replacement when $F = 0.16$ which corresponded to $A = 0.63$. When age-3 and older Burbot were targeted for removal, the population reached recruitment overfishing when $F = 0.22$ which corresponded to a mean $A = 0.64$.

In the absence of fishing mortality, the 10-year estimate of λ_G for Burbot in the Green River assuming high juvenile survival was 2.07 (2.04–2.12; Figure 4.6). When age-1 and older Burbot were fully selected for exploitation, the population growth rate reached recruitment overfishing when $F = 0.43$. An $F = 0.43$ corresponded to a mean $A = 0.70$ for age-1 and older Burbot. The population growth rate decreased below replacement at an $F = 0.69$ when age-2 and older Burbot were targeted for removal. An $F = 0.69$ would result in a mean $A = 0.76$ for age-2 and older Burbot. When age-3 and older Burbot were targeted for removal, the population never reached recruitment overfishing when F varied from 0–1.5.

The population growth rate was most sensitive to the survival of age-0 and age-1 Burbot (Figure 4.7). Assuming low juvenile survival, a 10% reduction in survival of age-0 Burbot resulted in a 40% reduction in the population growth rate over 10 years. With high juvenile survival, a 10% reduction in the survival of age-1 Burbot produced a 70% reduction in the population growth rate over 10 years.

Discussion

Information on population demographics provides valuable insight into population regulation and is necessary for effective management of fish populations (Guy and Brown 2007; Allen and Hightower 2010; Quist et al. 2012). In addition, demographics data are useful for understanding how Burbot in the Green River are responding to a novel habitat and how they will likely respond to management actions. Understanding the demography of Burbot in the Green River will help to identify the factors (i.e., habitat availability, prey availability) that most influence population regulation; thereby, allowing for the improved management of Burbot in other systems. Knowledge on Burbot populations is especially

needed in the southern extent of the species' distribution where low abundance and conservation status limit the amounts and types of data available to managers (Fischer 2008). Thus, demographic data are not only necessary for managing Burbot in the Green River, but are also useful for the management and conservation of Burbot populations throughout their distribution.

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

Body condition is valuable for evaluating the relative "robustness" of fishes and can provide insight into resource limitation (Ney 1993; Liao et al. 1995; Nuemann et al. 2012). For example, body condition of Largemouth Bass was positively correlated with prey biomass in Midwestern ponds (Wege and Anderson 1978). Similarly, Paukert and Willis (2003) reported a positive relationship between body condition of Northern Pike and prey abundance

in Nebraska lakes. Burbot in the Green River had similar condition to riverine populations within the species' native distribution. Fisher et al. (1996) reported that W_r of Burbot populations in 17 North American rivers averaged 79 for quality-, 79 for preferred-, 84 for memorable-, and 90 for trophy-length fish. In our study, W_r values for the autumn averaged 74 for quality-, 75 for preferred-, 77 for memorable-, and 88 for trophy-length Burbot. Fisher et al. (1996) suggested that due to environmental differences between lotic and lentic systems, the target relative weight of Burbot in lotic systems should be 80. Although slightly lower than the North American average, Burbot in the Green River are in very good condition. Similar to patterns observed with growth, these data suggest that prey resources are favorable to Burbot in the Green River.

Growth and condition influence the maturity and fecundity of fish in a population (Ferreri and Taylor 1996; Quist et al. 2012). Burbot generally reach sexual maturity around 400 mm (Chen 1969; Pulliainen and Korhonen 1990; Bernard et al. 1993), thus age-at-maturity is highly variable and dependent on individual growth. Evenson (1990) reported that female Burbot in the Tanana River, Alaska reached sexual maturity at age 6 (498 mm). Burbot in the Susquehanna River, New York reached sexual maturity between age 3 and 4 (240 mm–265 mm; Robins and Deubler 1955). Burbot in the Wind-Bighorn drainage generally reached sexual maturity at age 4, but length-at-maturity varied among water bodies (Hubert et al. 2008). For instance, Burbot in Trail Lake reached maturity at 246 mm; whereas, Burbot in Boysen Reservoir were sexually mature at 546 mm (Miller 1970). Burbot in the Green River reached sexual maturity at relatively young ages when compared to other populations. The early maturation of Burbot in the Green River is not surprising considering their relatively fast growth rate. Additionally, Burbot in the Green River were highly fecund

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

Fish populations not limited by resources are expected to maximize their reproductive output which is often reflected by fast growth, early maturation, and high fecundity (Rose et al. 2001). Ferreri and Taylor (1996) compared the Lake Trout population in Lake Superior, Michigan before and after the introduction of Sea Lamprey *Petromyzon marinus*. The authors reported that following the introduction of Sea Lamprey, Lake Trout were at lower abundance, grew faster, and had higher age-specific fecundity than the Lake Trout population prior to the introduction of Sea Lamprey. Burbot in the Green River grew faster, matured earlier, and had higher total fecundity than similar populations suggesting that the population is not limited by available resources. The fact that Burbot are not limited by available resources supports the finding that the population is growing.

The age-structured population model indicated that the Burbot population in the Green River will likely increase under current conditions. However, estimated population growth rates are based on a number of assumptions that may not reflect the true state of the Burbot population in the Green River. In particular, changes in juvenile survival would substantially

influence the population growth rate of Burbot in the Green River. The high estimate of age-0 survival used in population modeling was obtained from a study evaluating larviculture techniques for Burbot (Vught et al. 2008). The authors stocked larval Burbot into earthen ponds following yolk absorption and then evaluated mortality after nine months. In natural conditions, Burbot would likely suffer significant mortality during the egg and early larval stages due to biotic (e.g., predation) and abiotic (e.g., water temperature) factors; thus, the high estimates of juvenile survival used in population modeling likely overestimated the true population growth rate. Paragamian and Laude (2009) also evaluated survival of hatchery-reared juvenile Burbot in earthen ponds; however, Yellow Perch *Perca flavescens* were accidentally stocked into the pond and caused high mortality of juvenile Burbot. High juvenile mortality reported by Paragamian and Laude (2009) may be more similar to that of Burbot in the Green River which are subject to predation. Thus, estimates of population growth rate using low survival may better represent population growth of Burbot in the Green River. An additional assumption that may not be realistic is that of spawning frequency. Our population model assumed a “worst case scenario” where all of the mature female Burbot spawned every year. Spawning frequency of Burbot is highly variable, with reports varying from 60–95% of mature Burbot spawning in a given year (Pulliainen and Korhonen 1990; Evenson 1990; Pulliainen and Korhonen 1993). Although understanding spawning frequencies of Burbot is important for accurately describing population growth, any reduction in the current spawning frequency of Burbot in the Green River would ultimately result in a decrease from the current estimated population growth rate. Regardless of the uncertainties in model inputs, population metrics (e.g., age structure, age-at-maturity, and total fecundity) suggest that Burbot will likely persist in the Green River without intervention.

The age-structured population model indicated that the Burbot population in the Green River would require substantial levels of exploitation to reduce population growth rate below replacement ($\lambda < 1$). For example, achieving recruitment overfishing assuming only age-3 and older Burbot could be removed (assuming low survival) would require an $A = 0.58$. The total annual mortality rate needed to cause recruitment overfishing of Burbot in the Green River is similar to levels of mortality required to suppress other non-native fishes.

Simulations for non-native Lake Trout in Lake McDonald, Montana indicated that recruitment overfishing occurred when A was between 0.44 and 0.49 (Dux 2005). Similarly, Barbour et al. (2011) evaluated the potential removal of non-native Lionfish *Pterois volitans* from the western Atlantic Ocean, Caribbean Sea, and the Gulf of Mexico and concluded that an A of at least 0.60 would be needed to cause recruitment overfishing. Hansen et al. (2010) estimated that an A between 0.45 and 0.50 would be required to reduce non-native Lake Trout below replacement in Lake Pend Oreille, Idaho. Though possible, the cost associated with achieving high annual mortality rates represents a substantial economic investment. In Lake Pend Oreille alone, it costs approximately US\$400,000 annually to deploy trap and gill nets targeting non-native Lake Trout (Martinez et al. 2009). Given the considerable cost associated with suppressing non-native fish populations, any effort to increase the efficiency of removal efforts is beneficial to natural resource management agencies.

Sensitivity analysis indicated that targeting age-0 and age-1 Burbot would cause the greatest reduction in the population growth rate over 10 years. However, targeting younger age classes using established methods (e.g., hoop nets, electrofishing) may be difficult. For example, age-1 Burbot accounted for only about 4% of the total Burbot in our sample. It is unclear if these results are indicative of low capture efficiency or of low densities of juvenile

Burbot in the study area. Fisher (2000) reported that age-0 and age-1 Burbot used backwater habitats in the Missouri River, North Dakota. Additionally, Dillen et al. (2008) reported that larval and fingerling Burbot were sampled exclusively in tributaries of lowland rivers in France. Only the main channel of the Green River was sampled in our study; thus, the low number of Burbot sampled may be the result of differential habitat use of juvenile and adult Burbot. Nevertheless, future research should attempt to identify effective sampling techniques for juvenile Burbot and evaluate size-specific habitat use of Burbot.

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

contribute to the control of Burbot in the Green River, ultimately reducing the overall cost associated with removal efforts.

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

Results from this study indicate that Burbot grow fast, are in good body condition, mature early, and have high fecundity. The Burbot population in the Green River has likely not reached a point where density dependence is having a major influence on their population demographics and growth. Despite exponential population growth, the successful suppression of Burbot in the Green River is a tenable goal. However, care should be taken when designing and implementing a suppression program. Future research should attempt to fill knowledge gaps associated with vital rates used for population modelling, namely juvenile survival. Additionally, the difficulty associated with efficiently sampling Burbot necessitates future research into effective removal strategies. Angler exploitation and targeting spawning

aggregations represent two options to increase the efficiency of removal efforts, but by no means represent an exhaustive list. Therefore, future research should attempt to identify novel strategies for effectively removing Burbot in the Green River system.

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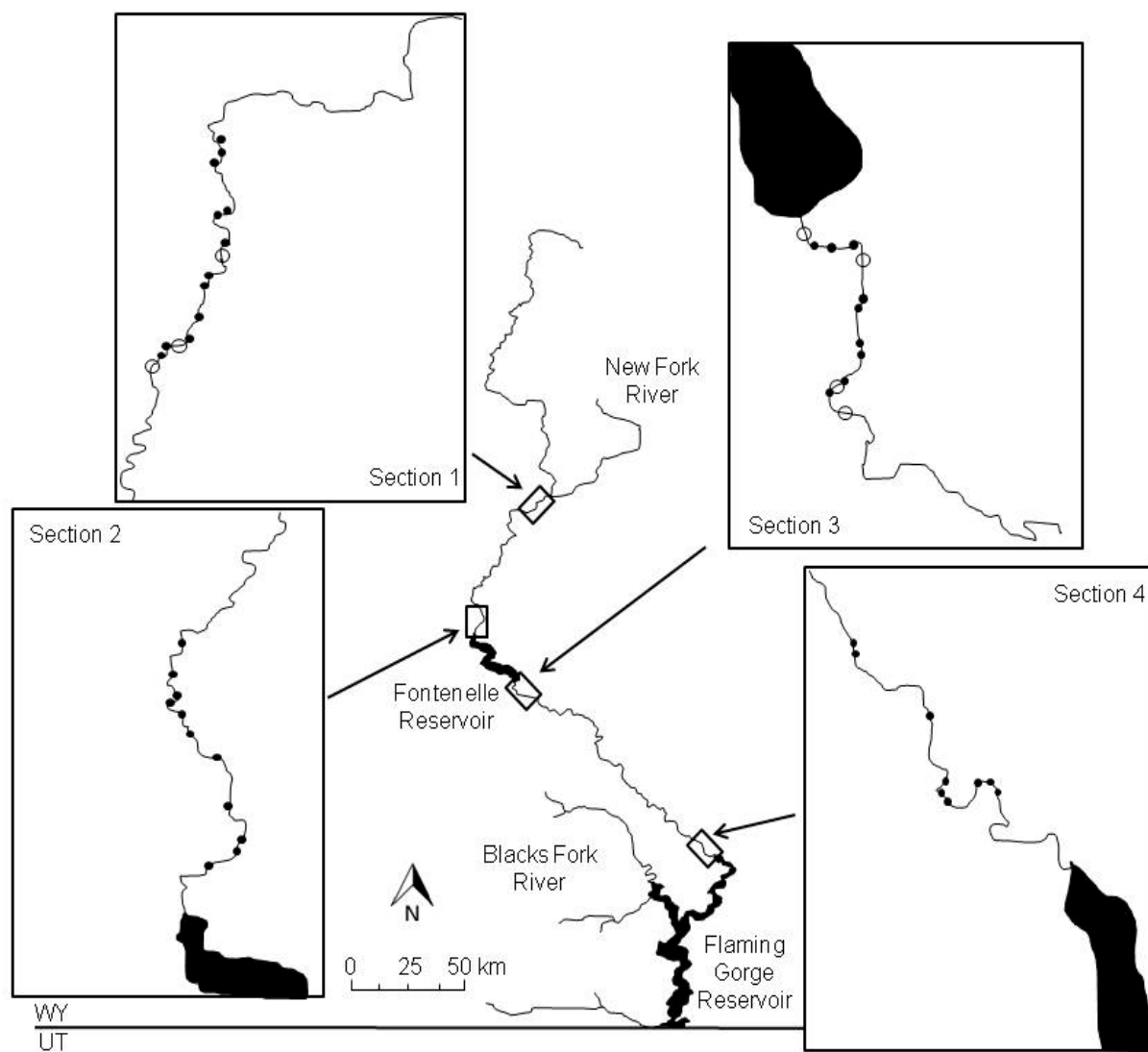
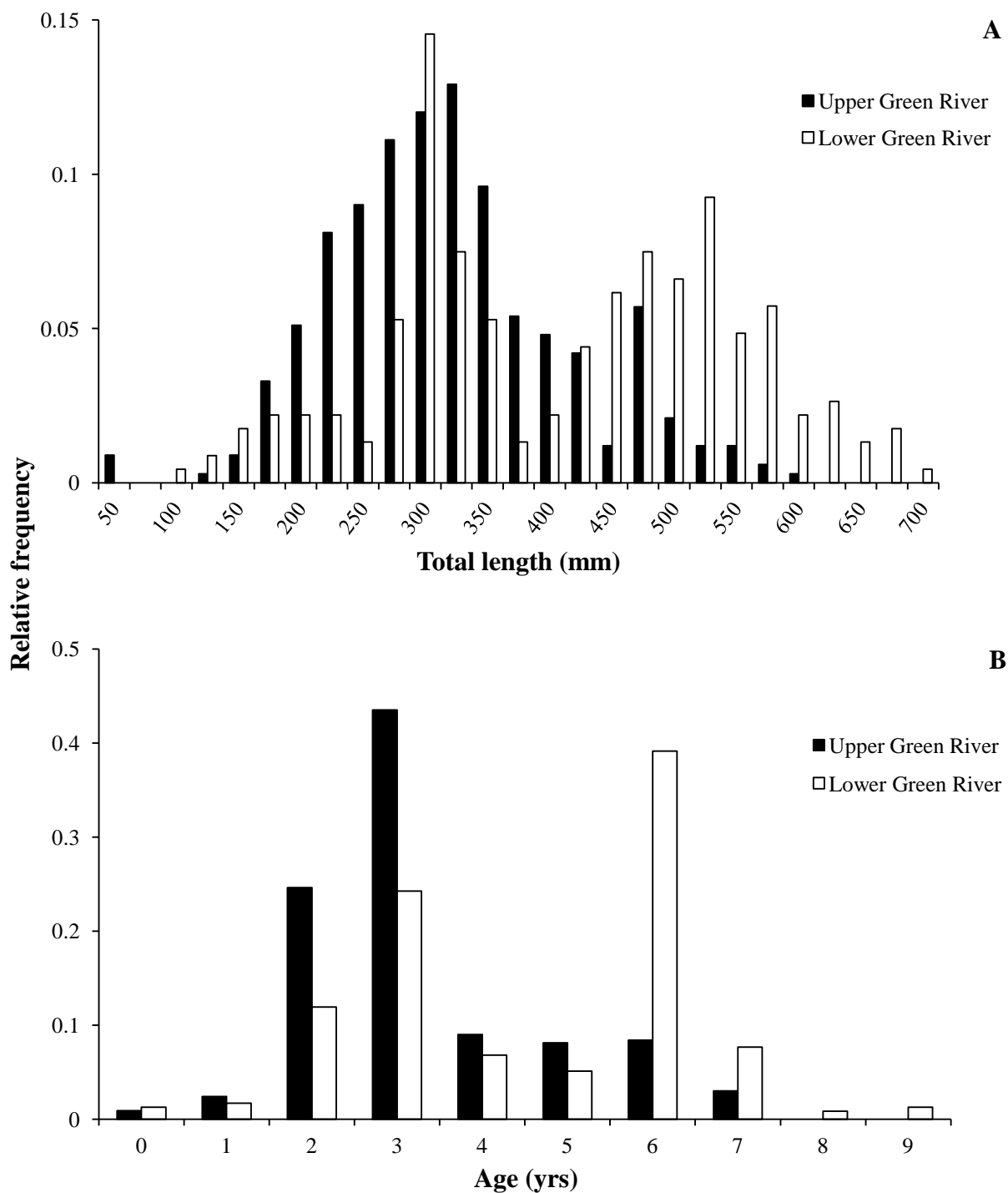
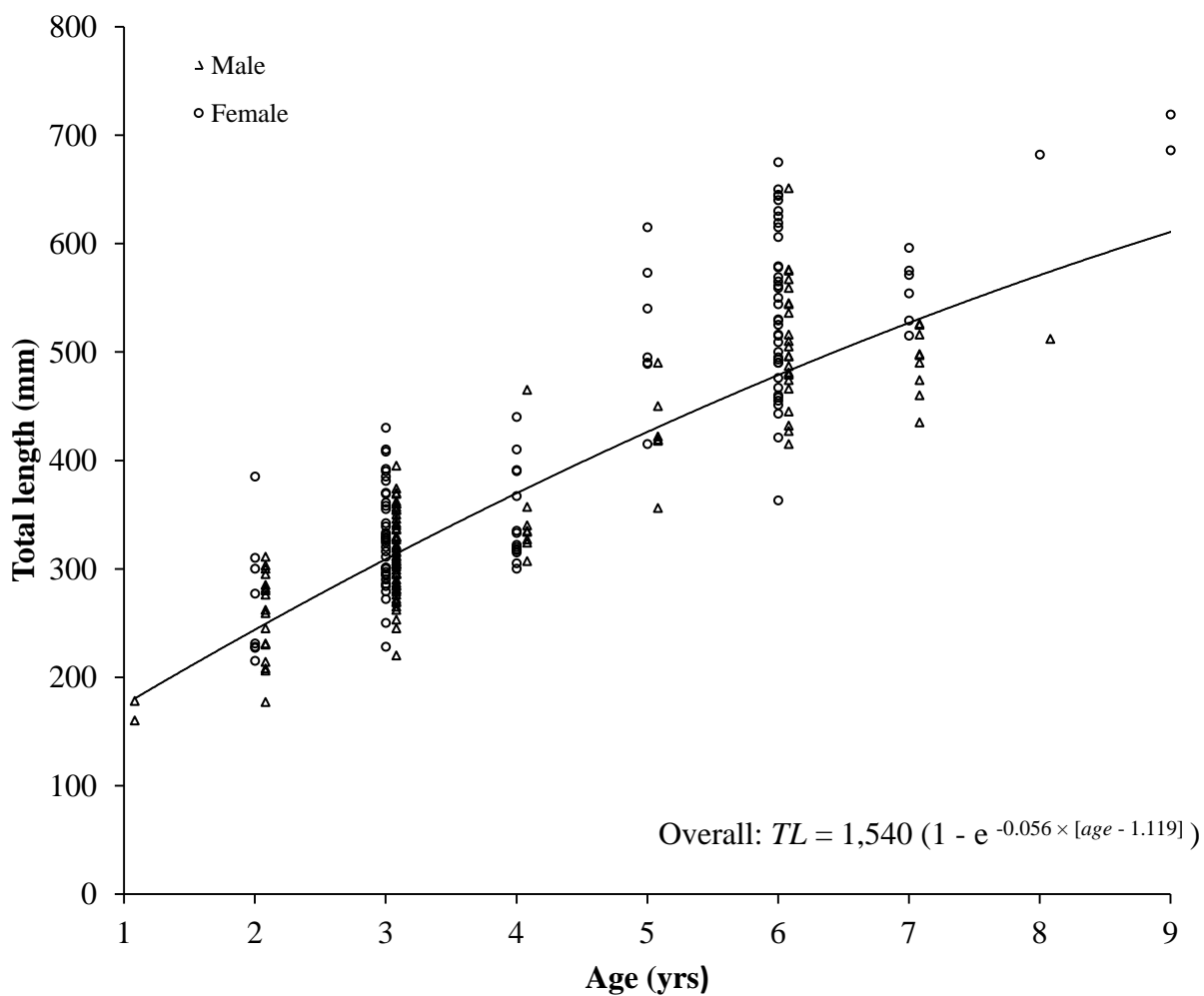


Figure 4.1. Sections used for Burbot sampling in the Green River, Wyoming during the summer and autumn (2013). Boxes depict each section in detail, with sites sampled in the summer (solid black circles) and sample sites added in autumn (open black circles).





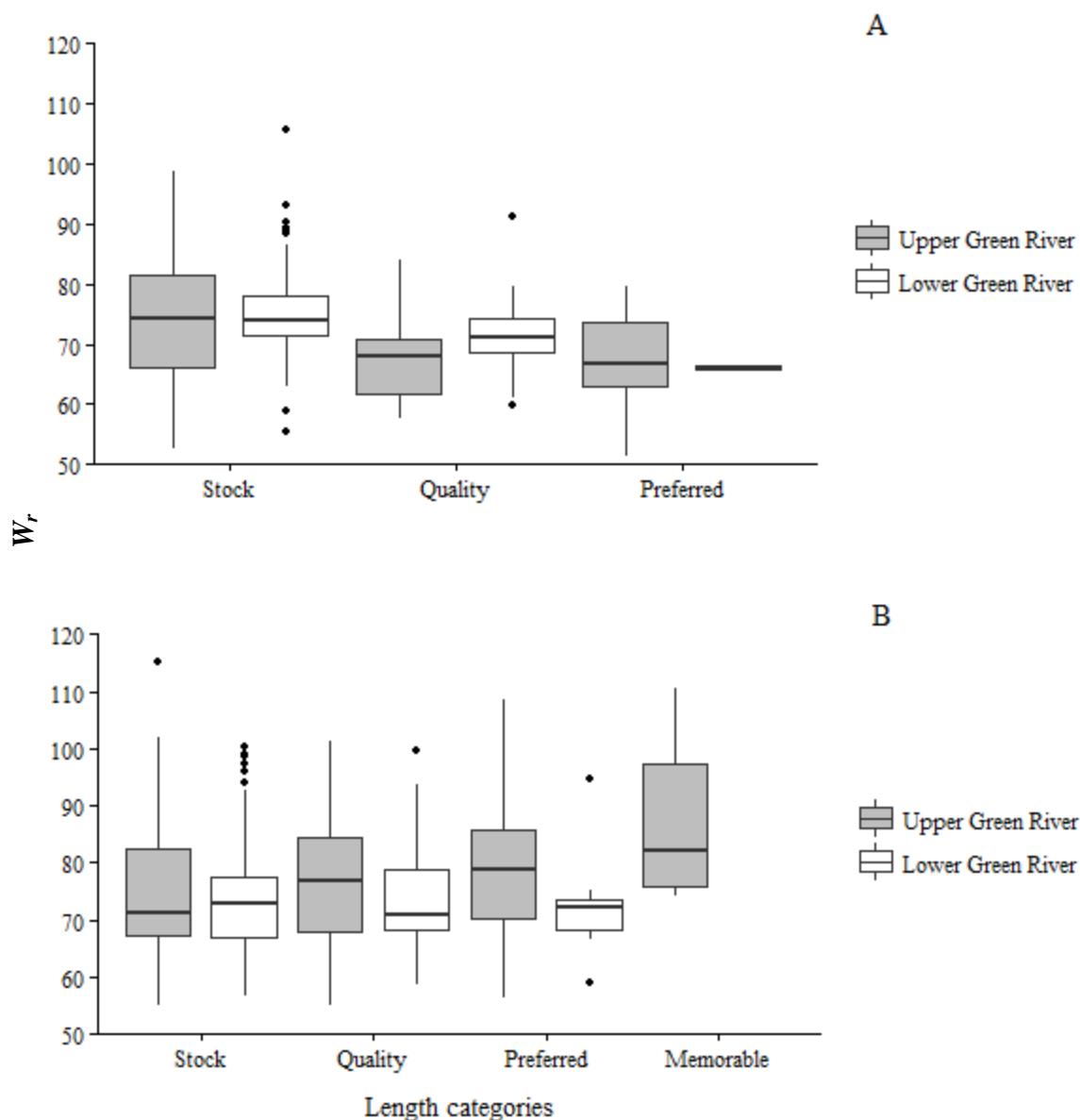


Figure 4.4. Boxplots of relative weight (W_r) by length category for Burbot sampled in the Green River, Wyoming during summer (A) and autumn (B; 2013). Reaches in the upper Green River are those upstream of Fontenelle Dam and those in the lower Green River are those downstream of Fontenelle Dam. Relative weights are included for stock- (≥ 200 mm), quality- (≥ 380 mm), preferred- (≥ 530 mm), and memorable-length (≥ 670 mm) Burbot.

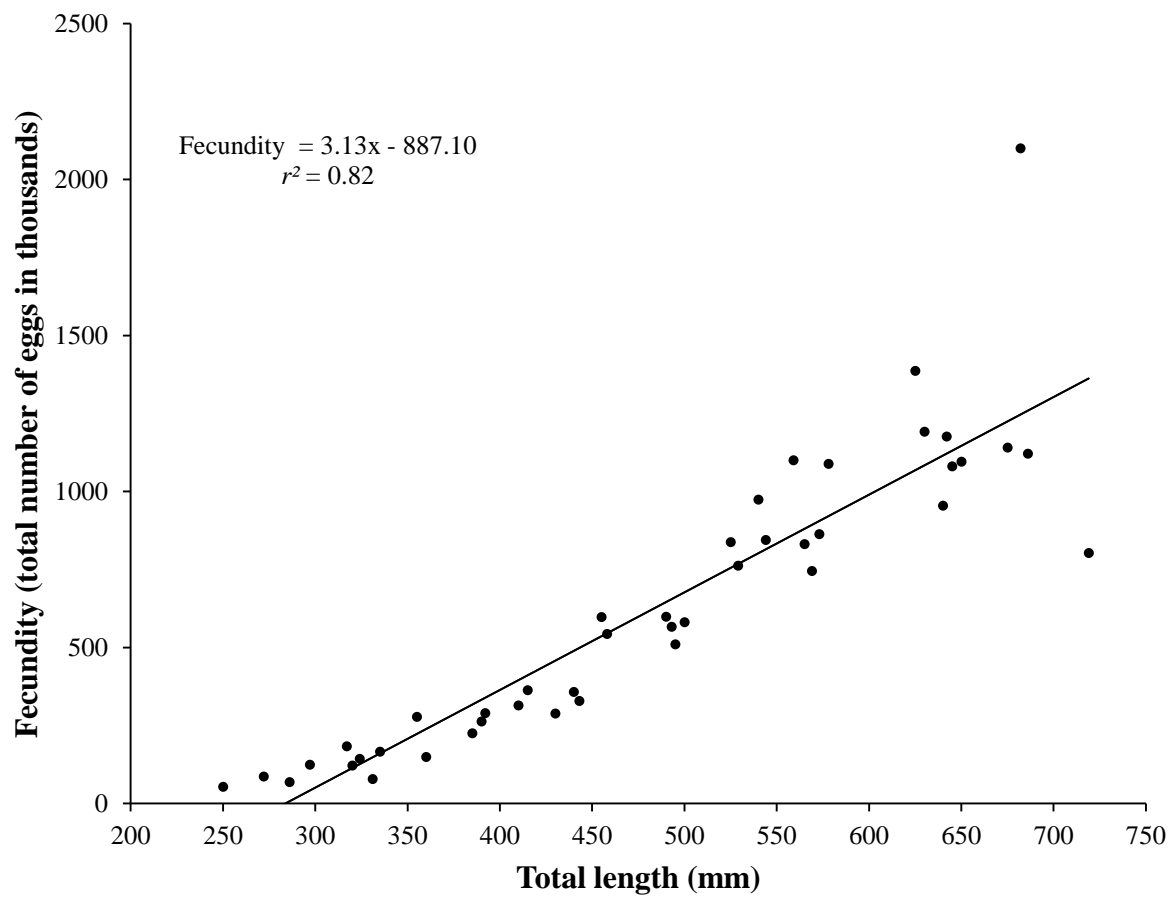


Figure 4.5. Fecundity-length relationship for Burbot sampled from the Green River, Wyoming during the autumn (2013). The solid line represents the fitted regression model.

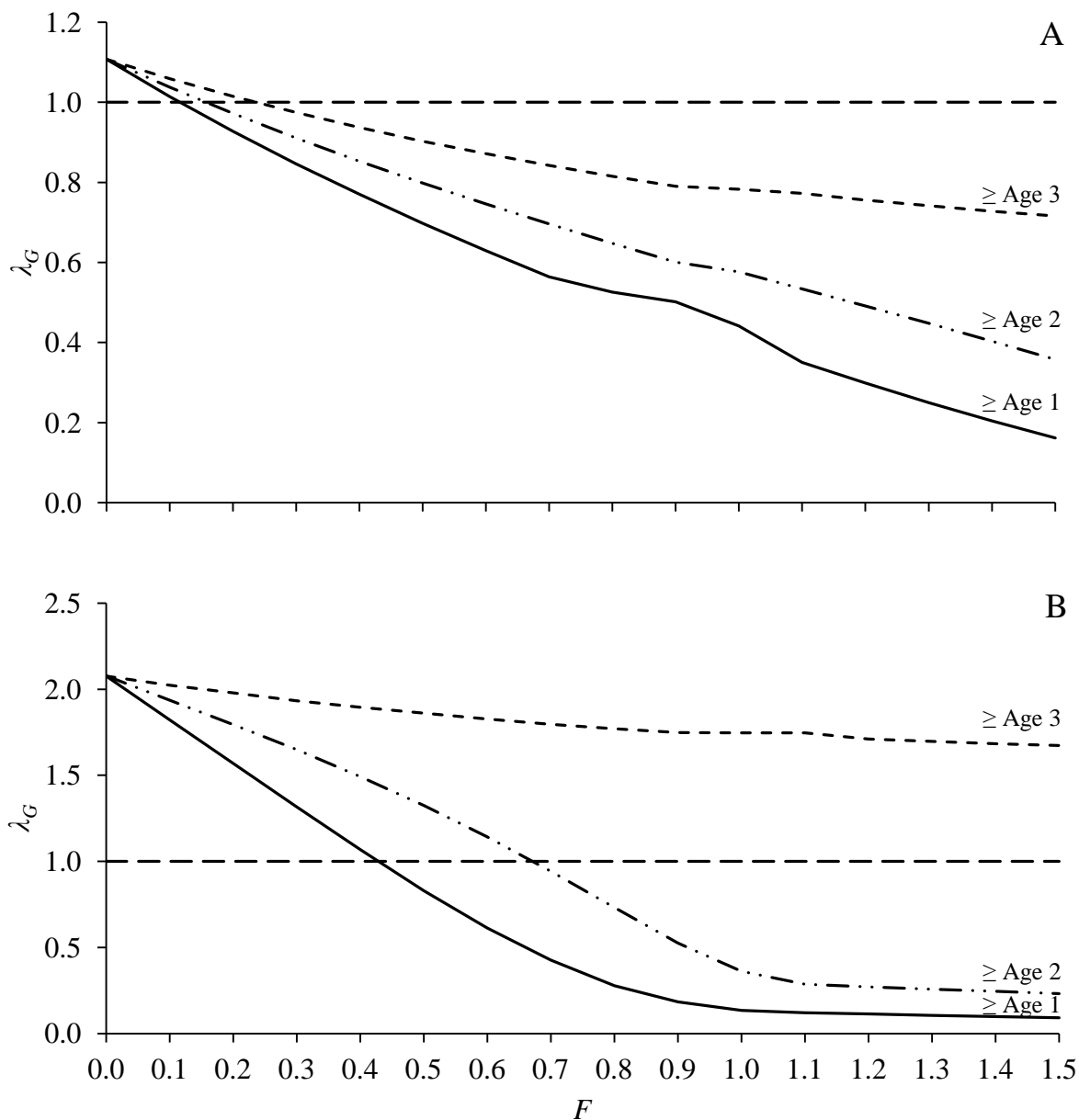


Figure 4.6. Population growth rate (λ_G) over a 10-year time frame for Burbot sampled from the Green River, Wyoming during the summer and autumn (2013). Population growth rate was calculated assuming low (A) and high (B) survival of age 0–2 Burbot and fully selected fishing mortality (F) for age-3 and older Burbot (dotted line), age-2 and older Burbot (dot-dashed line), and age-1 and older Burbot (solid line). The horizontal dashed line represents $\lambda_G = 1$ (replacement).

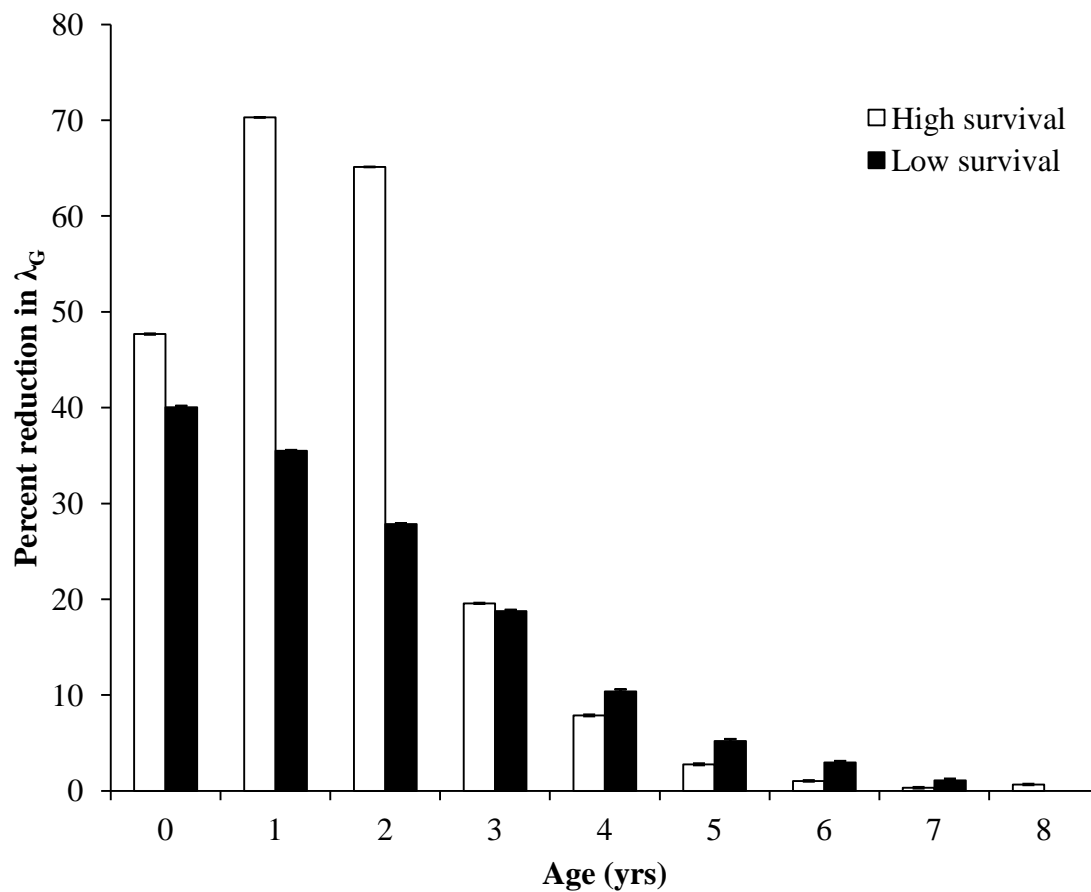


Figure 4.7. Percent reduction in geometric mean of population growth rate (λ_G) given 10% reductions in age-specific survival assuming high juvenile survival (no fill) and low juvenile survival (black fill) for Burbot in the Green River, Wyoming sampled during the summer and autumn, 2013. Error bars represent the standard errors. Reduction in population growth rate for age-9 Burbot assuming low and high survival was less than 0.001% and is not displayed.

Table 4.1. Mean vital rates and standard errors (SE) estimated from Burbot sampled from the Green River, Wyoming during the summer and autumn (2013). Vital rates and SE were used to construct population matrices.

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

Chapter 5: General Conclusions

Burbot are arguably one of the least-studied freshwater sport fish species in North America. Knowledge gaps surrounding the ecology of Burbot severely limit the ability of natural resource agencies to effectively manage the species. The broad goal of this thesis was to address the paucity of data associated with the ecology of the Burbot. The specific goal was to provide information to guide the suppression of Burbot in the Green River, Wyoming. Each chapter of this thesis addressed specific areas of Burbot management that were poorly understood and, thus, were limiting the efficacy of Burbot suppression in the Green River.

The findings of chapter two identified that small-mesh hoop nets and night electrofishing were more effective at sampling Burbot than large-mesh hoop nets. It should also be noted that trammel nets were originally included in the research; however, preliminary results suggested that trammel nets were impractical in the Green River due to the difficulty of keeping them stationary and rapid fouling by floating algae. Despite only comparing three sampling gears, previous research coupled with the findings of chapter two suggest that small-mesh hoop nets and night electrofishing are likely the most effective gears for sampling Burbot. Chapter three sought to evaluate the relationship between habitat characteristics and the occurrence and relative abundance of Burbot. Of the habitat characteristics measured, large substrate and areas of low current velocity were most often associated with the presence and relative abundance of Burbot in the Green River. In chapter four, I collected demographic data and used those data to evaluate how the Burbot population in the Green River would likely respond to various management actions. The age-structured population model indicated that about 60% of the population would need to be removed annually over 10 years to reduce the Burbot population in the Green River below replacement.

Although the control of Burbot in the Green River is a tenable goal, it does not represent the only management option for Burbot in the system. The suppression of Burbot in the Green River is postulated on the assumption that they are negatively influencing socially, economically, and ecologically important fishes. However, the negative influence of Burbot in the Green River has not been quantified. Due to the considerable cost associated with a long-term suppression program, the role of Burbot in the food web of the Green River should be well understood prior to implementing removal efforts. If the negative influence of Burbot on other fishes in the Green River is negligible, then the presence of Burbot may represent a unique opportunity; where, they can be managed as a sport fish. In addition to providing a unique fishing opportunity, Burbot in the Green River could facilitate additional research into the species ecology that is limited in other areas due to the species conservation status and (or) low abundance. Regardless of the specific management plan for Burbot in the Green River drainage, the first step to effective management is to understand the species' ecological role in the system. In doing so, managers will be able to make informed decisions on if suppression is necessary, and if so, they will have a better idea of the level of suppression needed to limit the deleterious effects of Burbot in the Green River.

Demographic data in conjunction with age-structured population models indicated that the suppression of Burbot will require a considerable amount of effort to achieve recruitment overfishing. Despite the amount of effort needed to achieve recruitment overfishing, the suppression of Burbot in the Green River is feasible. However, prior to implementing a suppression program for Burbot, it is advisable to understand the ecological role of Burbot in the Green River drainage. If controlling the abundance and distribution of Burbot in the Green River is the only plausible management scenario, then successful long-term

suppression relies on using the most effective gears to remove the largest number of individuals possible. By using small-mesh hoop nets and night electrofishing in habitats with large substrate and low current velocity, managers will likely have the greatest influence on the Burbot population in the Green River. To decrease the overall effort needed to suppress Burbot in the Green River, the Wyoming Game and Fish Department should target younger age classes and identify removal strategies that reduce the cost of long-term suppression. Regardless of the specific strategies used to control Burbot in the Green River, a sustained effort over 10 years that removes approximately 60% of the population annually is needed to reduce the non-native Burbot population in the Green River below replacement.

Appendix 5.1. Mean catch per unit effort (CPUE) and standard deviation (SD) for Burbot sampled in the Green River, Wyoming during the summer and fall (2013). Mean catch per unit effort by species is shown for small-mesh (HN_{6.4}) and large-mesh (HN₁₉) hoop nets for river section and sampling reach.

Season	Section	Gear	Reach	Species	Mean CPUE	SD
Summer	1	HN _{6.4}	1	BRT	0.016	0.028
				LND	0.097	0.168
				MSC	0.079	0.102
				RSS	0.968	1.635
				SPD	2.732	4.232
				WSH	0.354	0.456
			2	MSC	0.015	0.027
				RSS	0.031	0.053
				SPD	0.260	0.451
				WSH	0.017	0.030
			3	BRT	0.016	0.027
				SPD	0.029	0.026
				WSH	0.033	0.057
			4	BBT	0.014	0.024
				RSS	0.224	0.214
				SPD	0.318	0.276
				WSH	0.055	0.095
			5	LND	0.016	0.028
				RSS	0.129	0.224
				SPD	0.641	0.711
			6	SPD	0.015	0.026
			7	-	-	-

Appendix 5.1. cont'd

			8	BBT	0.029	0.025
				RSS	0.048	0.008
				SPD	0.188	0.148
				WSH	0.079	0.052
			9	MSC	0.014	0.024
				SPD	0.016	0.027
			10	BBT	0.018	0.031
				RSS	0.041	0.071
				SPD	0.121	0.176
			11	BBT	0.015	0.025
				MSC	0.015	0.026
				RSS	0.121	0.173
				SPD	0.267	0.234
			12	BBT	0.048	0.052
				RBT	0.016	0.027
				SPD	0.016	0.027
Summer	1	HN ₁₉				
			1	WSH	0.045	0.023
			2	-	-	-
			3	-	-	-
			4	-	-	-
			5	-	-	-
			6	-	-	-
			7	-	-	-

Appendix 5.1. cont'd

			8	-	-	-
			9	BBT	0.014	0.024
			10	-	-	-
			11	-	-	-
			12	BBT	0.015	0.026
				WSH	0.030	0.051
Summer	2	HN _{6,4}	1	BBT	0.029	0.050
				LND	0.043	0.074
				MSC	0.015	0.025
			2	MSC	0.015	0.026
				RSS	0.075	0.027
				SPD	0.286	0.262
				WSH	0.046	0.045
			3	MSC	0.030	0.026
				SPD	0.059	0.026
				WSH	0.015	0.026
			4	BBT	0.016	0.027
				RSS	0.028	0.048
				SPD	0.030	0.026
			5	CRW	0.061	0.053
				RSS	0.346	0.182
				SPD	0.483	0.196
				WSH	0.031	0.027
			6	BBT	0.073	0.027
				MSC	0.042	0.073

Appendix 5.1. cont'd

				RBT	0.013	0.023
				WSH	0.054	0.093
			7	BBT	0.069	0.120
				SPD	0.016	0.027
				WSH	0.032	0.028
			8	MSC	0.042	0.044
				RSS	0.662	0.541
				SPD	0.790	0.686
			9	RBT	0.015	0.026
				SPD	0.016	0.028
			10	BBT	0.043	0.074
				RBT	0.014	0.025
				RSS	0.014	0.024
				SPD	0.014	0.024
			11	MSC	0.033	0.029
				RSS	0.441	0.676
				SPD	0.315	0.271
				WSH	0.193	0.176
Summer	2	HN ₁₉	1	–	–	–
			2	–	–	–
			3	–	–	–
			4	BBT	0.015	0.026
			5	–	–	–
			6	–	–	–

Appendix 5.1. cont'd

			7	BBT	0.014	0.024
				WSH	0.014	0.024
			8	–	–	–
			9	–	–	–
			10	–	–	–
			11	WSH	0.069	0.088
Summer	3	HN _{6,4}	1	CRW	0.091	0.090
			2	CRW	0.134	0.078
			3	BBT	0.029	0.050
				CRW	0.048	0.084
			4	LND	0.015	0.026
			5	CRW	0.033	0.056
				LND	0.016	0.028
				WHS	0.016	0.028
			6	CRW	0.031	0.054
				LND	0.046	0.001
			7	LND	0.015	0.026
			8	BBT	0.015	0.026
				CRW	0.046	0.046
			9	BBT	0.031	0.054
				CRW	0.063	0.055
				WSH	0.016	0.027

Appendix 5.1. cont'd

Summer	3	HN ₁₉	1			
			2	CRW	0.016	0.027
			3	CRW	0.090	0.078
			4	–	–	–
			5	–	–	–
			6	CRW	0.046	0.079
				WSH	0.015	0.026
			7			
			8	WSH	0.015	0.027
			9	CRW	0.030	0.052
Summer	4	HN _{6,4}	1	BBT	0.031	0.053
				CRW	0.046	0.079
			2	–	–	–
			3	CRW	0.027	0.047
			4	BBT	0.060	0.069
				CRW	0.257	0.172
			5	BBT	0.060	0.023
				CRW	0.066	0.059
			6	BBT	0.015	0.026
				CRW	0.076	0.070
				WHS	0.031	0.053

Appendix 5.1. cont'd

			7	CRW	0.043	0.074
			8	CRW	0.143	0.147
				WHS	0.016	0.028
			9	BBT	0.014	0.024
				RSS	0.014	0.024
Summer	4	HN ₁₉	1	BBT	0.056	0.024
				BRT	0.015	0.025
			2	CRW	0.029	0.050
			3	CRW	0.079	0.100
				WSH	0.032	0.055
			4	CRW	0.042	0.072
			5	BBT	0.014	0.024
			6	–	–	–
			7	CRW	0.081	0.074
			8	BBT	0.012	0.020
			9	–	–	–
Fall	1	HN _{6.4}	1	BRT	0.013	0.023
				MWF	0.013	0.023
				SPD	0.066	0.114
				WSH	0.014	0.024
			2	BBT	0.014	0.024

Appendix 5.1. cont'd

	MSC	0.015	0.026
	RBT	0.027	0.047
	RSS	0.137	0.238
	SPD	0.442	0.728
3	WSH	0.041	0.042
4	BBT	0.043	0.045
	BRT	0.015	0.026
	RSS	0.015	0.026
	SPD	0.030	0.051
	WHS	0.118	0.071
5	BRT	0.027	0.046
	CRW	0.027	0.046
	MWF	0.013	0.023
	SPD	0.014	0.024
	WHS	0.014	0.024
6	BBT	0.015	0.027
	RSS	0.155	0.268
	SPD	0.031	0.054
	WHS	0.015	0.027
7	BBT	0.088	0.050
	SPD	0.014	0.023
	WHS	0.028	0.048
8	BBT	0.128	0.076
	MSC	0.015	0.026
	SPD	0.016	0.027
	WHS	0.026	0.045
9	BBT	0.115	0.065
10	BBT	0.026	0.044

Appendix 5.1. cont'd

			WHS	0.013	0.022
		11	BBT	0.014	0.024
			FMS	0.014	0.024
			SPD	0.014	0.024
		12	SPD	0.030	0.052
		13	BBT	0.029	0.025
			CRW	0.030	0.051
		14	BBT	0.044	0.046
			CRW	0.042	0.073
			RSS	0.014	0.024
			SPD	0.070	0.121
			WHS	0.099	0.134
		15	BBT	0.088	0.038
			BRT	0.031	0.053
			CRW	0.031	0.053
			MWF	0.015	0.026
			WHS	0.364	0.364
Fall	1	HN ₁₉			
		1	-	-	-
		2	-	-	-
		3	MSC	0.015	0.026
		4	WSH	0.041	0.040
		5	-	-	-
		6	-	-	-
		7	BBT	0.015	0.026

Appendix 5.1. cont'd

			8	BBT	0.040	0.069
			9	BBT	0.015	0.027
			10	–	–	–
			11	–	–	–
			12	–	–	–
			13	BBT	0.013	0.022
			14	BBT	0.030	0.026
			15	BBT	0.013	0.022
Fall	3	HN _{6,4}				
			1	BBT	0.081	0.047
				CRW	0.345	0.088
				RBT	0.027	0.047
				RSS	2.055	3.421
				UTC	0.081	0.081
				WHS	1.062	0.554
			2	CRW	0.976	0.479
				KOK	0.014	0.025
				RSS	0.083	0.083
				WHS	0.239	0.239
			3	CRW	0.783	0.573
				FMS	0.014	0.024
				RSS	1.635	1.742
				SPD	0.207	0.152
				UTC	0.028	0.024
				WHS	0.731	0.836
			4	BBT	0.014	0.024

Appendix 5.1. cont'd

	CRW	0.382	0.224
	RSS	0.196	0.265
	SPD	0.014	0.024
	WHS	0.785	0.929
5	CRW	0.124	0.072
	SPD	0.014	0.024
	WHS	0.055	0.023
6	BRT	0.028	0.048
	CRW	2.923	3.126
	RSS	0.014	0.024
	SPD	0.014	0.024
	WHS	0.349	0.604
7	BRT	0.014	0.024
	CRW	0.210	0.183
	RSS	2.351	1.981
	UTC	0.113	0.196
	WHS	2.187	3.644
8	CRW	1.863	0.881
	RBT	0.014	0.025
	RSS	1.127	0.831
	SPD	0.182	0.213
	UTC	0.028	0.048
	WHS	0.838	0.488
9	CRC	0.014	0.024
	CRW	1.737	1.858
	LND	0.028	0.049
	RSS	6.508	10.951
	SPD	0.329	0.255
	UTC	1.176	2.036
	WHS	1.152	1.276
10	CRW	0.862	0.339

Appendix 5.1. cont'd

			LND	0.056	0.060
			RSS	0.113	0.065
			SPD	0.028	0.024
			UTC	0.014	0.024
			WHS	0.467	0.225
		11	CRW	5.685	3.154
			WHS	0.014	0.025
		12	BBT	0.070	0.065
			CRW	0.496	0.315
			RSS	0.014	0.025
			SPD	0.014	0.025
			WHS	0.172	0.297
		13	BBT	0.014	0.024
			CRW	0.356	0.365
			SPD	0.014	0.023
			WHS	0.041	0.070
Fall	3	HN ₁₉			
			1	CRW	0.028
				UTC	0.014
			2	CRW	0.189
			3	CRW	0.272
				WHS	0.014
			4	CRW	0.137
				WHS	0.041
			5	BBT	0.014
				CRW	0.042
			6	CRW	0.574
				WHS	0.014

Appendix 5.1. cont'd

7	CRW	0.155	0.158
	WHS	0.084	0.084
8	BBT	0.014	0.024
	CRW	0.415	0.247
	WHS	0.028	0.049
9	CRW	0.709	0.790
	WHS	0.028	0.025
10	CRW	0.166	0.037
	WHS	0.014	0.024
11	BRT	0.014	0.024
	CRW	0.340	0.319
12	BBT	0.013	0.023
	CRW	0.216	0.191
	WHS	0.014	0.024
13	BBT	0.018	0.024
	CRW	0.418	0.211
	WHS	0.029	0.049
