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BURBOT ECOLOGY

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.

Keywords Burbot · Habitat use · Suppression · Hurdle regression

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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 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; Berthou, 2007; Baxter et al., 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 *Catosomus discobolus* Cope, flannelmouth sucker *Catosomus latipinnis* Baird & Girard, roundtail chub *Gila robusta* Baird & Girard; WGFD, 2010; Gardunio et al., 2011). Despite these concerns, 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.

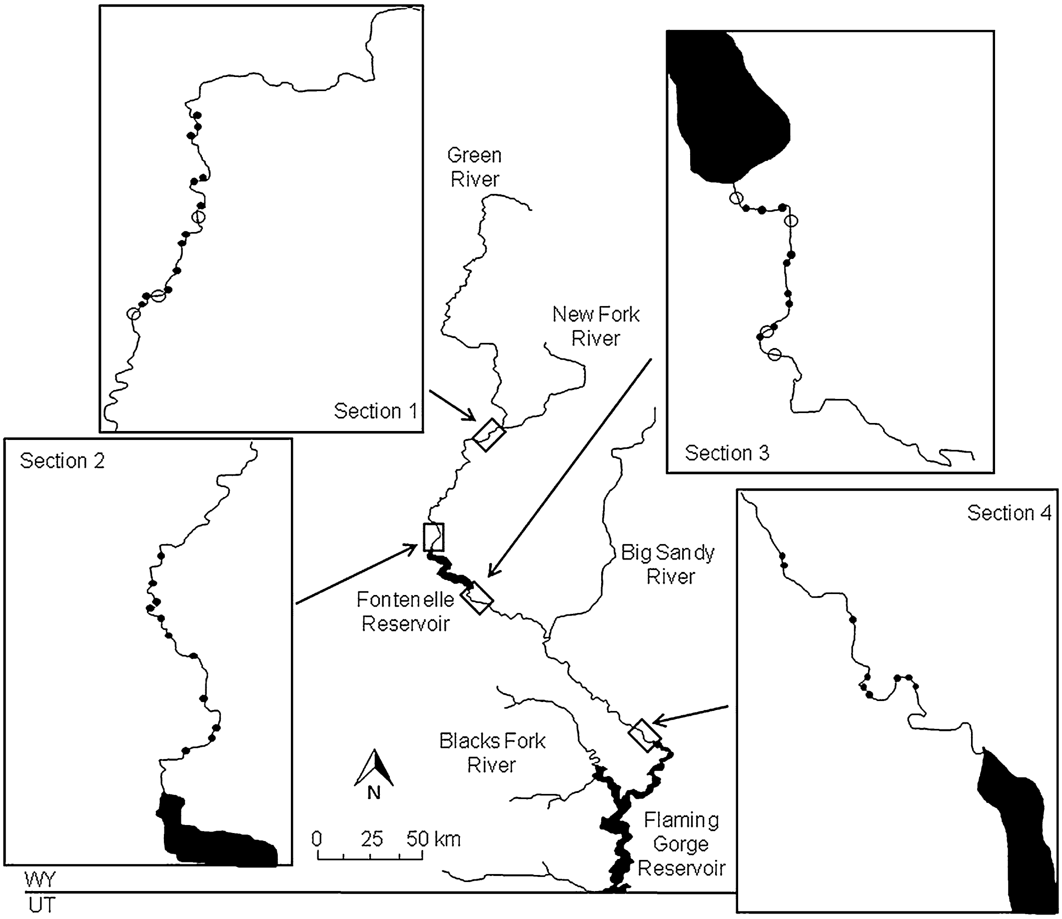

Fig. 1 Sections used for juvenile and adult burbot sampling in the Green River, Wyoming during the summer and autumn (2013). Boxes depict each section in detail with sites sampled in the summer (i.e., *solid black circles*) and sample sites added in autumn to increase sample size (i.e., *open black circles*)

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 area

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. 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).

Materials and 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. 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 3 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., 3 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. 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 × 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 × 41 cm square opening covered with a 36 cm × 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 h. 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 electrofishing 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, and 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, and 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, and bank type). Channel-unit length and width were measured to the nearest 0.5 m using a laser range-finder. In-stream habitat characteristics were measured along a diagonal transect from the uppermost 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 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, MN). 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 (64.0–26.0 mm), boulder (>27.0 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 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, and 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 (°C), conductivity (μS/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 ($\mathrm{AIC_c}$; Burnham & Anderson, 2002). Models with the lowest $\mathrm{AIC_c}$ value were considered the most supported models from each suite of candidate models. Overdispersed models were ranked using quasi-$\mathrm{AIC_c}$ ($\mathrm{QAIC_c}$) and an additional parameter was added to further penalize overdispersed candidate models (Burnham & Anderson, 2002). All models with a $\Delta\mathrm{AIC_c}$ or $\Delta\mathrm{QAIC_c}$ 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 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

Table 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)

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)
$\text{Depth}_{\text{Mean}}$	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)
$\text{Velocity}_{\text{Mean}}$	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)
$\text{Substrate}_{\text{Co–Bl}}$	Percentage of cobble and boulder substrate (Proportion)	0.53 (0.10)	0.81 (0.08)	0.83 (0.09)	0.12 (0.06)	0.63 (0.06)	0.93 (0.06)
$\text{Substrate}_{\text{Bl}}$	Percentage of boulder substrate (Proportion)	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 (Proportion)	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 (Proportion)	0.03 (0.02)	0.13 (0.05)	0.64 (0.10)	0.00 (0)	0.19 (0.06)	0.48 (0.06)
$\text{Bank}_{\text{Bluff}}$	Percentage of alluvium bluff bank (Proportion)	0.14 (0.06)	0.14 (0.07)	0.15 (0.07)	0.29 (0.08)	0.17 (0.06)	0.22 (0.06)
$\text{Bank}_{\text{Eroded}}$	Percentage of eroded bank (Proportion)	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 (Proportion)	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 (h)	43.50 (0.20)	45.33 (0.26)	44.08 (0.16)	46.68 (0.53)	46.45 (0.16)	47.88 (0.08)

River Section 1 is the most upstream section followed by Sections 2, 3, and 4

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 ± 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 press). The mean length of burbot sampled increased from the summer (mean length ± 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 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, and 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 embeddedness, 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 embeddedness, 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

Table 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)

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

Akiake's information criterion ($\mathrm{AIC_c}$) or quasi-Akiake's information criterion adjusted for small sample size ($\mathrm{QAIC_c}$) 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 $\Delta\mathrm{AIC} < 2$ and the most parameterized model (italics) in each candidate set are included velocity ($\leq$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 min at a current velocity of 25 cm/s. Similarly, Paragamian (2000) reported that the upstream movement of prespawn 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 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 Ohŕe 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 embeddedness. 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 (Paragamian, 2000; Hubert et al., 2008). Additionally, both the Wind-Bighorn and Kootenai rivers have experienced substantial water development in the last 100 years (Paragamian, 2000; Hubert et al., 2008). 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 "under-used" niche. 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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