Open Access

Research Article

Comparison of burbot populations across adjacent native and introduced ranges

Annika W. Walters[1],*, Elizabeth G. Mandeville[2], W. Carl Saunders[3], Paul C. Gerrity[4], Joseph A. Skorupski[5], Zack E. Underwood[6] and Eric I. Gardunio[7]

[1]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, 1000 E. University Avenue, University of Wyoming, Laramie, Wyoming 82071, USA

[2]Department of Botany, 1000 E. University Avenue, University of Wyoming, Laramie, Wyoming 82071, USA

[3]Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, Utah, 84322, USA

[4]Wyoming Game and Fish Department, 260 Buena Vista Drive, Lander, Wyoming 82520, USA

[5]Wyoming Game and Fish Department, 2820 State Highway 120, Cody, Wyoming 82414, USA

[6]Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, 1000 E. University Avenue, University of Wyoming, Laramie, Wyoming 82071, USA

[7]Colorado Parks and Wildlife, 2300 S. Townsend Ave., Montrose, CO 81401, USA

Author e-mails: annika.walters@uwyo.edu (AWW), emandevi@uwyo.edu (EGM), Carl.Saunders@usu.edu (WCS), paul.gerrity@wyo.gov (PCG), joe.skorupski@wyo.gov (JAS), zeunderwood@gmail.com (ZEU), eric.gardunio@state.co.us (EIG)

*Corresponding author

Abstract

Introduced species are a threat to biodiversity. Burbot, *Lota lota,* a fish native to the Wind River Drainage, Wyoming and a species of conservation concern, have been introduced into the nearby Green River Drainage, Wyoming, where they are having negative effects on native fish species. We compared these native and introduced burbot populations to evaluate potential mechanisms that could be leading to introduction success. We examined genetic ancestry, physical habitat characteristics, community composition, and burbot abundance, relative weight, and size structure between the native and introduced range to elucidate potential differences. The origin of introduced burbot in Flaming Gorge Reservoir is most likely Boysen Reservoir and several nearby river populations in the native Wind River Drainage. Burbot populations did not show consistent differences in abundance, size structure, and relative weight between drainages, though Fontenelle Reservoir, in the introduced drainage, had the largest burbot. There were also limited environmental and community composition differences, though reservoirs in the introduced drainage had lower species richness and a higher percentage of non-native fish species than the reservoir in the native drainage. Burbot introduction in the Green River Drainage is likely an example of reservoir construction creating habitat with suitable environmental conditions to allow a southwards range expansion of this cold-water species. An understanding of the factors driving introduction success can allow better management of species, both in their introduced and native range.

Key words: *Lota lota*, invasive species, non-native, range expansion, invasion success

Introduction

Introduced species can have substantial negative effects on aquatic communities through predation, habitat modification, and competition (Kulhanek et al. 2011). However, most species that are introduced outside their native range do not become abundant in their new range (Mack et al. 2000). Understanding the mechanisms underlying successful introduction is therefore the focus of considerable theoretical and empirical research (Budy et al. 2013; Gurevitch et al. 2011; Lowry et al. 2013). The results of this body of research indicate that the mechanisms for introduction success are often context specific, but generally relate to characteristics of the introduced fish, biotic and abiotic components of the environment, fish-environment match, disturbance, and characteristics of the introduction (Catford et al. 2009; Mack et al. 2000; Ruesink 2005).

Comparisons between native and introduced populations can provide insight into the mechanisms that lead to introduction success, especially when the native

Table 1. Potential hypotheses for burbot introduction success in the Green River Drainage, and predictions for Green River drainage burbot in contrast to Wind River drainage burbot if the hypothesis was supported.

Category	Hypothesis	Explanation	Predictions for Green River Drainage	References
Burbot traits	Evolution of increased competitive ability	Fewer natural enemies results in reduction in resources for defense and towards increased competitive ability	Increasing abundance, higher condition and larger burbot	(Blossey and Notzold 1995; Bossdorf et al. 2005; Budy et al. 2013)
Environment traits	Empty niche	Low biodiversity in an ecosystem will result in increased chances of successful introduction because of empty niches and high resource availability	Lower species richness	(Knops et al. 1999; Shurin 2000; Stachowicz et al. 2002)
	Disturbance	Higher success in habitats with moderate levels of disturbance because of increased availability of resources in disturbance patches	More disturbed habitat (reservoir habitat, high % non-natives)	(Colautti et al. 2006; Renne et al. 2006; Sher and Hyatt 1999)
Burbot – environment match	Habitat filtering	Introduced species is successful if it is adapted to environmental conditions of ecosystem	More high quality habitat (deep, cold)	(Fausch 2008; Melbourne et al. 2007; Weiher and Keddy 1995)

and introduced habitats occur in close proximity so one can control for biogeography. Species often differ in their population dynamics and demographics between native and introduced habitats. For example, brook trout *Salvelinus fontinalis* (Mitchill, 1814) are declining in parts of their native range (Marschall and Crowder 1996; Stranko et al. 2008), but are a highly successful invader displacing cutthroat trout *Oncorhynchus clarki* (Richardson, 1836) in the western United States (Fausch 2008; Peterson et al. 2004). Similarly, brown trout *Salmo trutta* (Linnaeus, 1758) reach a larger maximum body size and are more piscivorous in their introduced range (Budy et al. 2013).

In Wyoming, burbot, *Lota lota*, (Linnaeus, 1758) are native to the Wind River Drainage, but were illegally introduced into the Green River Drainage in the early- to mid-1990s (Gardunio et al. 2011). While this only represents a slight range expansion, it places burbot in a new major river drainage—the Colorado River. The Colorado River drainage has historically much lower fish species richness than the Missouri River drainage, and contains a number of fish species of high conservation concern, such as the flannelmouth *Catostomus latipinnis* (Baird and Girard, 1853), bluehead *Catostomus discobolus* (Cope, 1871), and razorback *Xyrauchen texanus* (Abbott, 1860) suckers. There is limited continuous data on burbot abundances in their native range, but there is concern about potential declines due to angler exploitation and habitat modification (Hubert et al. 2008; Krueger and Hubert 1997; Lewandowski 2015). However, burbot populations in their introduced range have expanded rapidly and are the target of substantial eradication efforts (Gardunio et al. 2011). The success of these introduced populations is surprising as the introduced population represents a southern expansion. Globally burbot populations at the southern edge of their distribution have been in decline and are vulnerable to extirpation due to warming temperatures (Stapanian et al. 2010).

We hypothesize that burbot introduction success in the Green River Drainage may be related to burbot traits, environment traits, or burbot-environment match and present four potential hypotheses (Table 1). The first is the "evolution of increased competitive ability", in which the lack of natural enemies allows introduced burbot to focus resources towards increased competitive ability instead of defense (Blossey and Notzold 1995; Budy et al. 2013). The next two relate to the environment. The "empty niche" hypothesis suggests that lower biodiversity in an ecosystem will increase introduction success (Shurin 2000; Stachowicz et al. 2002). The "disturbance" hypothesis suggests that there will be higher success in more disturbed habitats due to increased availability of resources (Renne et al. 2006; Sher and Hyatt 1999). Lastly the "habitat filtering" hypothesis considers species-environment match, and suggests success will be due to the presence of high-quality environmental conditions to which burbot are already adapted (Fausch 2008; Melbourne et al. 2007).

Our goal is to better understand the potential mechanisms driving the expansion of burbot in their introduced range by comparing burbot populations in the Wind and Green River drainages. To provide
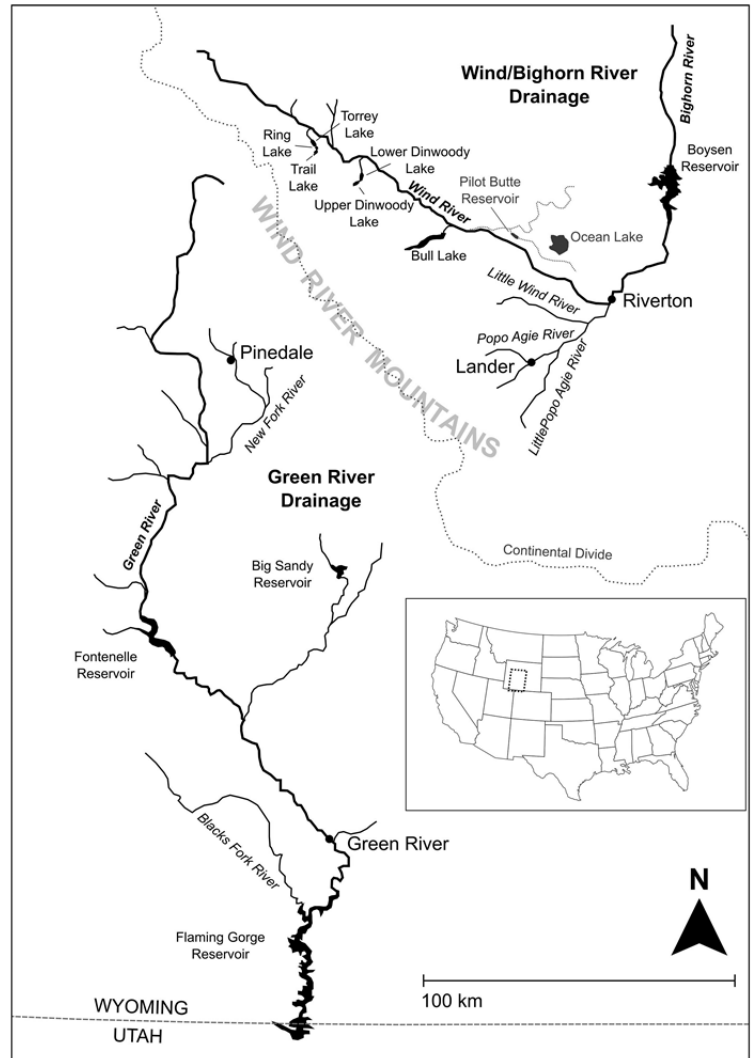
Figure 1. The Wind River (native burbot populations) and Green River (introduced burbot populations) drainages in southcentral Wyoming, USA. The inset figure identifies the location of the drainages within the United States.

context for comparison of native and introduced populations, we use genetic data to determine the likely origin of introduced burbot in the Green River Drainage. We then use available data to compare lake and reservoir physical characteristics, community composition, and burbot abundance, relative weight, and size structure between the native and introduced range. Our objective is to elucidate potential differences between the burbot populations and evaluate the support for each of the hypothesized mechanisms for burbot success in the Green River Drainage (Table 1). An understanding of the factors driving population dynamics of burbot within their native and introduced range could help inform management: both control and suppression in the introduced range, and conservation and potential restoration in the native range.

Methods

Study area

Burbot are found in lakes, reservoirs, and rivers. Native populations are found within the Wind River Drainage in tributary lakes of the Wind River, Boysen Reservoir, and in low numbers in the Wind River above Boysen Reservoir and lower portions of the Little Wind, Popo Agie, and Little Popo Agie rivers (Figure 1). The tributary lakes were formed during the Quaternary ice-age and were likely colonized by Missourian lineage burbot sometime after the recession of the Bull Lake and Pinedale glaciations, 21,000 years ago. Stable populations are currently present within Torrey, Ring and Trail lakes on Torrey Creek; Upper and Lower Dinwoody lakes on Dinwoody Creek; and in Bull Lake on Bull Lake

Table 2. Physical characteristics of lakes and reservoirs inhabited by burbot in the introduced Green River (Fontenelle and Flaming Gorge reservoirs) and native Wind River (Boysen Reservoir and Bull, Lower Dinwoody, Ring, Trail, Torrey, and Upper Dinwoody lakes) drainages, Wyoming. Elevation, surface area, and depth data are from the Bureau of Reclamation http://www.usbr.gov/ for Green River drainage sites and from Hubert et al. (2008) for Wind River drainage sites. Air temperature data (average 2000–2011) for all sites were gathered from the Water Resources Data System http://www.wrds.uwyo.edu/sco/data/PRISM/PRISM.html.

	Type of water body	Elevation at full pool (m)	Max SA[1] at full pool (ha)	Max depth at full pool (m)	Mean July air temp.[2] (°C)
Flaming Gorge Reservoir	Reservoir	1841	17005	133	21.7
Fontenelle Reservoir	Reservoir	1985	3261	37	18.6
Boysen Reservoir	Reservoir	1445	7916	35	24.6
Bull Lake	Modified natural lake	1775	1300	45	20
Lower Dinwoody Lake	Modified Natural lake	1980	400	61	17.8
Ring Lake	Natural lake	2261	39	9	16.6
Trail Lake	Natural lake	2267	49	11	16.6
Torrey Lake	Natural lake	2259	94	18	16.6
Upper Dinwoody Lake	Natural lake	1982	171	14	17.8

[1]Surface area

[2]We report mean July air temperature as this is representative of warmer summer temperatures. In addition, in Northern Hemisphere temperate regions July is when mean air and surface water temperatures correspond most closely (Livingstone and Lotter 1998).

Creek (Figure 1; Abrahamse 2008; Hubert et al. 2008). Burbot are also abundant in Boysen Reservoir which was formed by the construction of Boysen Dam on the Wind River in 1952.

Introduced populations are found in the Green River Drainage (Figure 1). Burbot were first documented in Big Sandy River, a tributary to the Green River, in 2001. They were subsequently documented in Fontenelle Reservoir in 2005 and in Flaming Gorge Reservoir in 2006. Currently burbot are established throughout the Green River Drainage, including the New Fork, Green, and Big Sandy rivers, and Fontenelle, Flaming Gorge, and Big Sandy reservoirs (Gardunio et al. 2011).

There is considerable variation in the size (39–17005 ha) and depth (9–133 m) of the lakes and reservoirs inhabited by burbot (Table 2). Flaming Gorge Reservoir is more than twice as large and deep as any of the other lakes/reservoirs. Fontenelle Reservoir is also large, but is comparable to lakes/reservoirs in the Wind River Drainage such as Boysen Reservoir and Bull Lake. The Ring, Trail, and Torrey lakes are the smallest and shallowest. They are also at the highest elevations so experience the coolest July air temperatures. Boysen Reservoir experiences the warmest July air temperatures.

Genetics

As part of an ongoing investigation of population genetic structure of burbot within Wyoming, we generated and analyzed high throughput DNA sequence data for 271 burbot from 11 locations in the Wind River drainage, plus 5 Flaming Gorge

Reservoir burbot. We report on the Wind River data more fully in another manuscript (Underwood et al. 2016). Any fish we collected were handled under Wyoming Game and Fish Department permit number 901 and Institutional Animal Care and Use protocol #20140404AW00087-02. For this study, the goal of our genetic analysis was to understand how introduced burbot in Flaming Gorge Reservoir compare to burbot populations in their native range. We used a genotyping by sequencing approach. Reduced complexity genomic libraries were prepared according to protocols in Parchman et al. (2012) and sequenced on the Illumina Hiseq 2500 platform at the University of Texas Genome Sequencing and Analysis Facility (UT-GSAF, Austin, TX).

Following assembly and variant calling to identify variable genetic sites (SNPs: single nucleotide polymorphisms), we used individual-based analyses to confirm that each geographically defined population corresponded to a genetic cluster (methods detailed in Underwood et al. (2016), and similar to Mandeville et al. (2015)). We then applied a population-based model, TreeMix (Pickrell and Pritchard 2012), to better understand genetic relationships among populations. For this analysis, we used data at 11,278 SNPs to calculate population allele frequencies and allele counts at each genetic site. TreeMix is a likelihood-based model that detects population divergences and historical mixture events between populations, resulting in a distance tree overlaid with proposed gene flow events between populations that improve model fit. This maximum likelihood tree shows genetic relationships among burbot populations.

Population and community dynamics

We gathered burbot data for lakes and reservoirs within the Wind River and Green River drainages from published literature, Master's theses, and internal reports from the Wyoming Game and Fish Department (WGFD). The WGFD has conducted standardized burbot sampling in Boysen Reservoir since 2005 and in Fontenelle and Flaming Gorge (collected in conjunction with the Utah Division of Wildlife Resources (UDWR)) reservoirs since 2006. We only used data from 2008 onward as during the first years of sampling there were some inconsistencies in gear placement for some sites. Sampling occurred during spring in Boysen Reservoir and during fall in Fontenelle and Flaming Gorge reservoirs. Sampling was conducted using trammel nets set overnight (16–22 hours) on steep, rocky substrate found along shorelines of the reservoirs. Trammel nets were 48.8 m long and 1.8 m deep with outer panels of 25.4-cm bar mesh and inner panels of 2.5-cm bar mesh. Burbot less than 270 mm were rarely caught in the nets, but larger size classes were consistently represented. At Boysen Reservoir, trammel nets were set at six standard sites. In Flaming Gorge, nets were set at nine standard sites (three each in northern (inflow), central (open hills), and southern (canyon) region). In Fontenelle Reservoir, three nets were set at standard sites. Mean catch per unit effort (CPUE; fish h^{-1}) was used as our index of burbot population abundance. We used linear regression of CPUE against year for each reservoir to assess potential trends in abundance. We plotted a histogram of the residuals and the residuals against fitted values for each linear model to assess whether the models met the assumptions of normality and homogeneity of variance. We also tested for autocorrelation of residuals using an acf plot since we were working with time-series data. We saw no concerning trends in the residuals. All plots and analyses were carried out in R (R Core Team 2014).

We examined size structure based on burbot length data from the WGFD and UDWR standardized burbot sampling for Boysen, Fontenelle, and Flaming Gorge reservoirs, and data from Lewandowski (2015) for other sites in the Wind River drainage. We restricted our analysis to burbot caught in 2011, 2012, and 2013 since those were the years in which data was available for the Wind River lakes. For all lakes except Ring Lake there were at least 100 fish sampled. We examined mean length, standard deviation of length, and the proportion of fish found in each standard length category. Minimum lengths used for stock, quality, preferred, memorable, and trophy size class burbot were 200 mm, 380 mm,

530 mm, 670 mm, and 820 mm, respectively (Fisher et al. 1996). We ran a linear mixed effects model with drainage as the fixed effect and site nested within drainage as the random effect to examine whether length varied by drainage with the nlme package (Pinheiro et al. 2014). We also conducted an analysis of variance (ANOVA) examining whether length varied by site and year and conducted a post-hoc analysis Tukey test to compare site and year pairs. We plotted a histogram of the residuals and the residuals against fitted values to assess whether the models met the assumptions of normality and homogeneity of variance, and saw no concerns.

Relative weight (W_r), an index of body condition, was calculated from WGFD and UDWR monitoring data for Boysen, Fontenelle, and Flaming Gorge reservoirs. Relative weight was calculated according to Anderson and Neumann (1996):

$$Log_{10}(W_s) = a + b(log_{10}(L))$$
$$W_r = 100 \ (W/W_s)$$

where W_s = standard weight, a = intercept, b = slope, L = fish length, W_r = relative weight, and W = fish weight. Values for burbot for the intercept (a = −4.868, metric) and slope (b = 2.898) were taken from Fisher et al. (1996). We calculated W_r for fish collected during 2011, 2012, and 2013. We removed from analyses 5 fish that had relative weight scores lower than 50, as these were extreme outliers. We used an ANOVA to examine whether relative weight varied by site and year and conducted a post-hoc analysis Tukey test to compare site and year pairs. To examine the relationship between relative weight and length we used a linear regression of relative weight against length for each site. For both sets of models we plotted a histogram of the residuals and the residuals against fitted values to assess that the model residuals were normally distributed and had homogenous variance, and saw no concerning trends in the residuals.

Fish community composition for Green River and Wind River drainages was based on presence and absence of fish species as determined through WGFD and UDWR monitoring for 2005–2015.

Results

Genetics

Burbot from Flaming Gorge Reservoir in the Green River Drainage are genetically most similar to those from Boysen Reservoir and several nearby river populations (Little Wind, Little Popo Agie) (Figure 2).

Population and community dynamics

Mean burbot CPUE ranged from 0.34 to 1.28 fish hour^{-1} and standard deviation was high, especially for
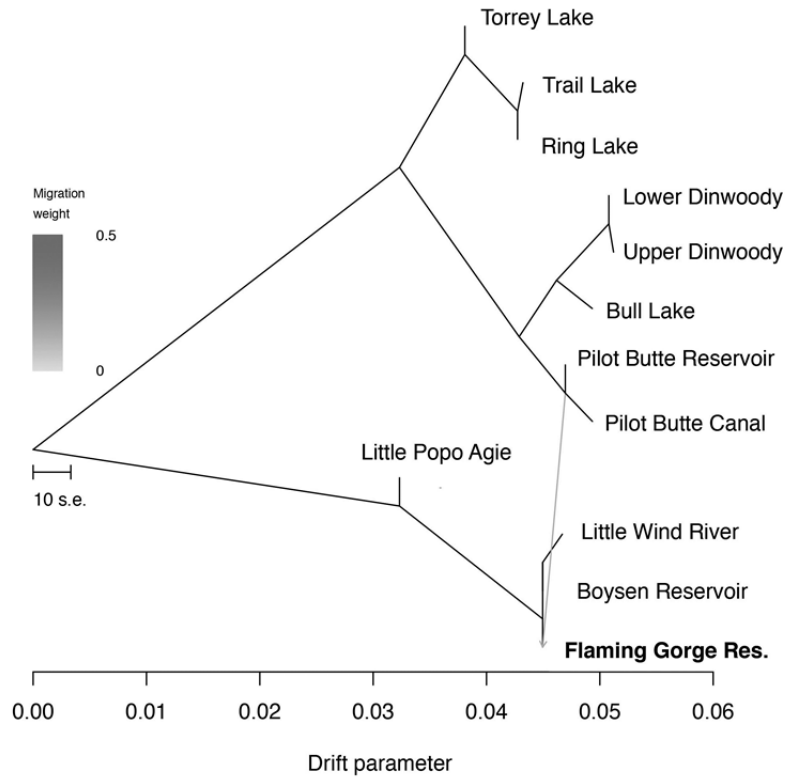
Figure 2. Relationships among sampled populations in a maximum likelihood tree suggest that introduced burbot in Flaming Gorge Reservoir were probably moved from Boysen Reservoir. Boysen Reservoir and Flaming Gorge burbot are nested within the Lower Wind River populations. The arrow represents probable gene flow from the upper Wind River populations to the lower Wind River populations.
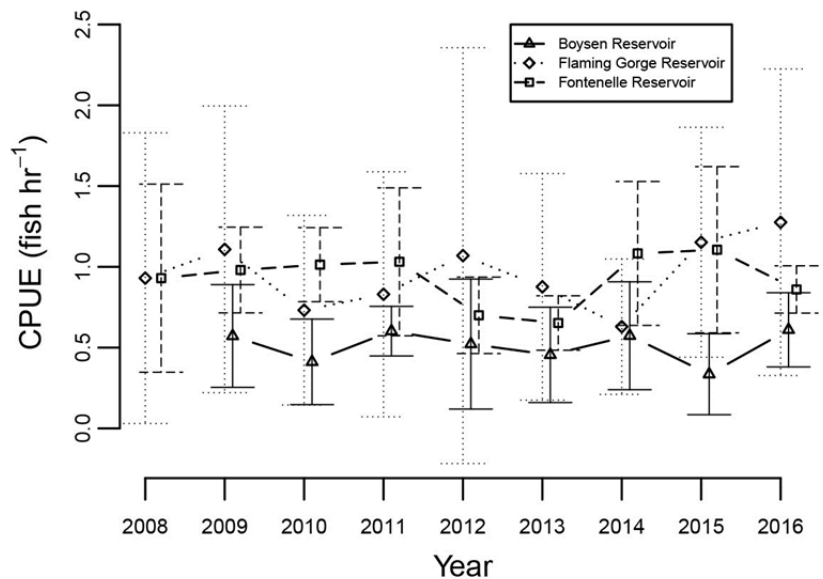

Figure 3. Burbot mean catch per unit effort (CPUE; fish hour^{-1}) $\pm$ standard deviation from standardized trammel net surveys for Boysen (native, 6 nets), Fontenelle (introduced, 3 nets), and Flaming Gorge (introduced, 9 nets) reservoirs from 2008 to 2016. Boysen Reservoir was not sampled in 2008, only 4 nets were sampled in Boysen Reservoir in 2013, and only 2 nets were sampled in Fontenelle Reservoir in 2011.

Flaming Gorge (Figure 3). CPUE in Flaming Gorge and Fontenelle reservoirs was around 1.0 fish hour^{-1}, while in Boysen Reservoir it was just above 0.5 fish hour^{-1}. There were no significant trends in CPUE by year for Boysen (slope = 0, $F_{1,6}$ = 0.04, P = 0.85),

Flaming Gorge (slope = 0.02, $F_{1,7}$ = 0.66, P = 0.44), or Fontenelle (slope = 0, $F_{1,7}$ = 0.01, P = 0.92) reservoirs.

Mean burbot length varied from 376 to 638 mm with Fontenelle Reservoir having the largest mean length. Variation was high (standard deviation: 72–223)
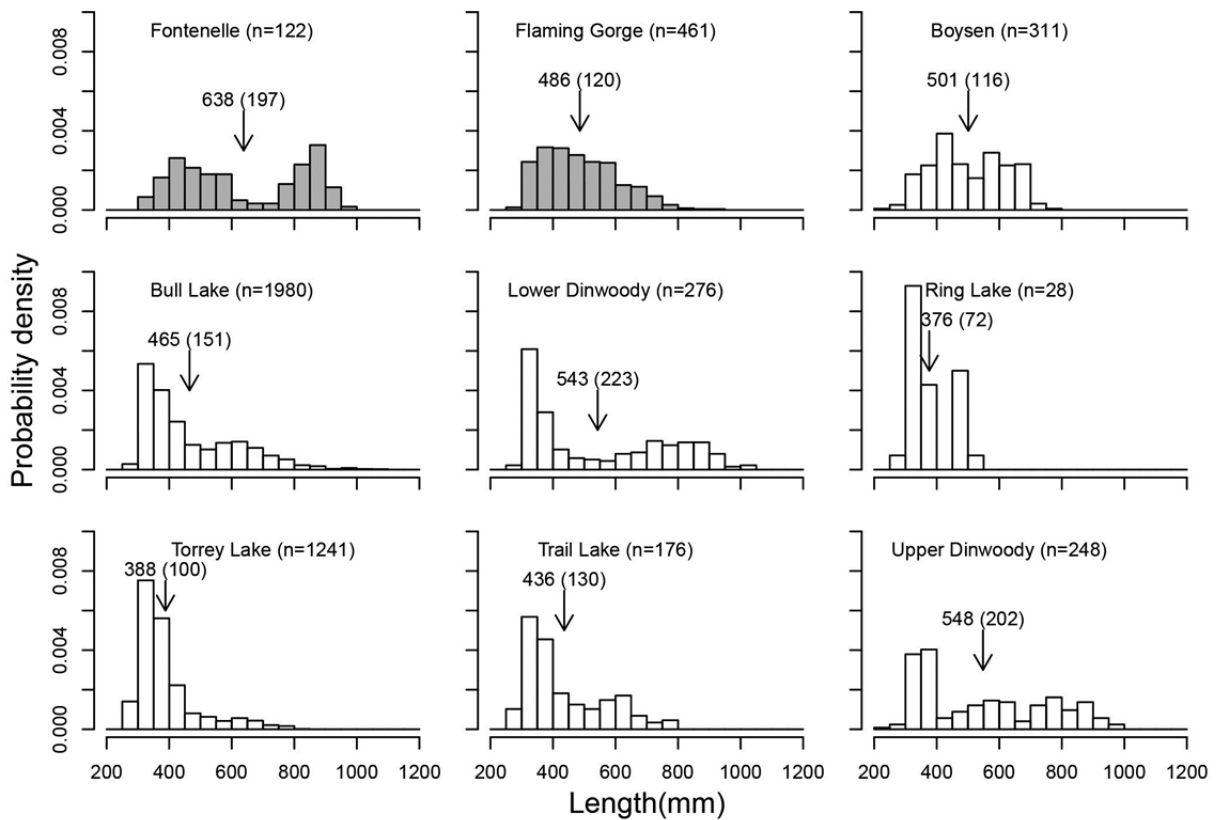
Figure 4. Histograms of burbot length for each population; the arrow denotes the mean (standard deviation) length. Introduced population histograms are in gray.

and several populations showed a bi-modal distribution of lengths (Figure 4). Bull, Ring, Trail and Torrey lakes had a large proportion (40–65%) of small burbot (stock size, <380 mm) and almost no trophy fish (0–2%, 820+ mm). Fontenelle Reservoir, Lower Dinwoody Lake and Upper Dinwoody Lake had the largest proportion of trophy fish, with a third of the Fontenelle Reservoir fish falling in this size class. Length was lower for the Wind River drainage than the Green River drainage, but not significantly ($t_7 = -1.56$, $P = 0.16$). However, mean burbot length varied significantly by year ($F_{1,4833} = 199.32$, $P<0.001$) and among individual lakes/reservoirs ($F_{8,4833} = 96.56$, $P<0.001$). A post-hoc Tukey test found fish in 2011 were larger than fish in 2012 ($P<0.001$), which were larger than fish in 2013 ($P<0.001$). Fontenelle Reservoir had larger fish, on average, than all other sites ($P<0.001$), while fish in Flaming Gorge Reservoir were, on average, smaller than those from Lower Dinwoody and Upper Dinwoody lakes ($P<0.001$),

but larger than fish found in Ring, Torrey, and Trail lakes ($P<0.01$).

All reservoir sites in both native and introduced range had mainly burbot of relative weight less than 100 (Figure 5). The effect of year ($F_{2,834} = 3.44$, $P = 0.03$) and site ($F_{2,834} = 123.92$, $P<0.001$) on relative weight was significant. A post-hoc Tukey test found that 2013 had fish of higher relative weight than 2012 ($P = 0.02$), but there was no difference between 2011 and 2012 ($P = 0.45$) or 2011 and 2013 ($P = 0.37$). Burbot in Flaming Gorge and Fontenelle reservoirs had similar relative weight ($P = 0.20$), but Boysen Reservoir had burbot of higher relative weight ($P<0.001$; Figure 5). The higher relative weight of burbot in Boysen Reservoir was driven by higher relative weight in the smaller size classes, with relative weight declining for larger fish (slope $= -0.04$, $F_{1,260} = 45.57$, $R^2 = 0.15$, $P<0.001$; Figure 5). These smaller, high relative weight fish in Boysen were primarily captured in 2013. Flaming Gorge showed the
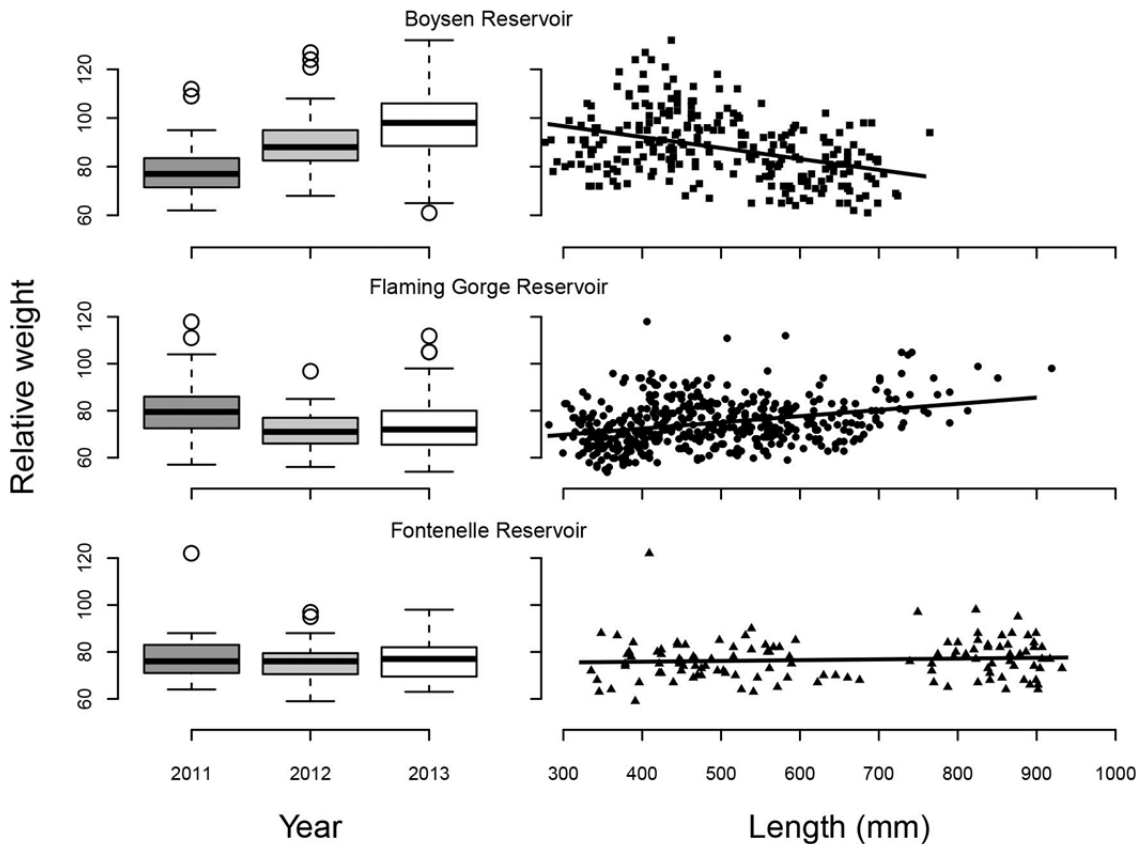
Figure 5. Burbot relative weight broken down by year and in relation to length for (Boysen native), Flaming Gorge (introduced), and Fontenelle (introduced) reservoirs.

Table 3. Number of native and nonnative species present in the introduced Green River (Fontenelle and Flaming Gorge reservoirs) and native Wind River (Boysen Reservoir and Bull, Lower Dinwoody, Ring, Trail, Torrey, and Upper Dinwoody lakes) drainages, Wyoming.

Fish species	Fontenelle Reservoir	Flaming Gorge Reservoir	Boysen Reservoir	Bull Lake	Lower Dinwoody Lake	Ring Lake	Trail Lake	Torrey Lake	Upper Dinwoody Lake
Native species	5	5	16	7	7	6	6	6	7
Nonnative species	8	9	14	8	5	5	5	5	5
Total species richness	**13**	**14**	**30**	**15**	**12**	**11**	**11**	**11**	**12**
% Nonnative	**62%**	**64%**	**47%**	**53%**	**42%**	**45%**	**45%**	**45%**	**42%**

opposite pattern with larger fish having higher relative weight (slope = 0.03, $F_{1,455}$ = 50.62, R^2 = 0.10, P<0.001), while Fontenelle Reservoir showed no trend (slope = 0, $F_{1,118}$ = 0.66, R^2 = 0, P = 0.42).

Boysen Reservoir had the highest species richness (30) which was double that of any other lake/reservoir (Table 3, Supplementary material Table S1). Fontenelle and Flaming Gorge species richness (13–14) was comparable to the other Wind River lakes (11–15), but Fontenelle and Flaming Gorge reservoirs had a higher proportion of nonnative species (Table 3).

Discussion

Characteristics of the environment and burbot-environment match are the most likely factors driving burbot introduction success in the Green River drainage. While burbot populations showed substantial variability in abundance, size structure, and relative weight, the variability was not consistently related to drainage providing no support for the "evolution of increased competitive ability" hypothesis (Table 1). There were some differences

in physical habitat characteristics and community composition between drainages providing limited support for the "empty niche" and "disturbance" hypotheses. For example, Flaming Gorge and Fontenelle reservoirs had lower species richness than Boysen Reservoir and the highest percentage of non-native fish species. We were limited by data availability for assessing the "habitat filtering" hypothesis, but the presence of deep habitat in the Green River drainage suggests there is high-quality cold habitat available for burbot. This is surprising as the Green River drainage populations represent a southwards range expansion for a cold stenothermal species. However, human alteration of these systems has created temporally stable coldwater habitats, including dam tailwater sections and deep reservoirs, which are likely ideal for burbot.

The Flaming Gorge burbot included in genetic analyses in this study, probably all have ancestry from a single source population, and are genetically similar to burbot sampled from the lower Wind River populations, including Boysen Reservoir. Although we present only the TreeMix analysis here, these results are consistent across multiple genetic analyses of individuals and populations, and are associated with low uncertainty (Underwood 2015). Boysen Reservoir is the most likely source as the river populations are at very low densities and fishing for burbot primarily occurs on lakes in the winter. The finding of limited genetic differentiation provides context for the comparisons. Given that Boysen Reservoir is likely the primary source of burbot in Flaming Gorge Reservoir, the comparison of abundance and size structure between Boysen and Flaming Gorge Reservoir is highly appropriate.

There were no large differences in burbot CPUE, size structure, or relative weight between Boysen Reservoir and the introduced populations in Fontenelle and Flaming Gorge reservoirs, though Fontenelle Reservoir had the highest proportion of trophy size fish. Burbot condition was relatively low, but it has been suggested that reservoir burbot generally have lower relative weight (Fisher et al. 1996). However, three to nine years of data is a relatively short time period for characterizing population dynamics and demographics. The Fontenelle and Flaming Gorge populations are relatively recent introductions so are likely still moving towards equilibrium dynamics. The CPUE numbers do not account for the substantial management effort to control and reduce burbot numbers in the Green River Drainage, including a "must kill" provision for all burbot caught and fishing events targeted at burbot. The CPUE data is also limited by the assumption of constant capture probability. The timing of sampling varied among reservoirs, but the limited instances where both spring and fall trammel net data are available (WGFD data for Boysen in 2004 and Flaming Gorge Inflow in 2006, Abrahamse 2008) do not suggest consistent trends with sampling time. In addition, both time periods correspond to cold water conditions when burbot are most active (Hofmann and Fischer 2002; Holker et al. 2004). Given that there has been no detailed evaluation of population demographics for burbot in the area, the data used are the best available.

Despite the relatively stable CPUE numbers, burbot are highly successful in the Green River drainage where they have been able to establish and spread (Gardunio et al. 2011). Burbot are not known to be widely introduced and are declining across much of their native range (Stapanian et al. 2010). However, it was noted in the 1951 version of Wyoming Fishes "to keep it (burbot) confined to drainages to which it is native since potentially it is a harmful fish if planted indiscriminately" (Simon 1951). The lack of widespread burbot range expansion may therefore be due to the lack of introduction attempts rather than a lack of appropriate traits. Burbot have several traits thought to be important for introduction success including very high fecundity: a female can produce from 6300 to 3.4 million eggs (Stapanian et al. 2010). This high fecundity, coupled with a long life-span could help burbot establish in new environments. In addition, larval burbot have a pelagic life stage that could help with range expansion (McPhail and Paragamian 2000). Burbot also have broad dietary preferences (Jacobs et al. 2010; Klobucar et al. 2016) and a fairly high thermal tolerance for a cold-water fish (Hofmann and Fischer 2002; Paakkonen et al. 2003).

For some introduced species, there has been support for the "evolution of increased competitive ability" hypothesis (Blossey and Notzold 1995; Whitney and Gabler 2008). For example, brown trout are larger and more piscivorous in their non-native range (Budy et al. 2013). We did not observe larger burbot of higher relative weight in the Green River Drainage, but it may also be too early to tell if something similar could occur with burbot. Burbot do appear to be very adept at switching between prey resources in response to variation in prey availability (McPhail and Paragamian 2000; Klobucar et al. 2016).

We only have very coarse scale data available to examine environmental characteristics that could be important for introduction success (Catford et al. 2009) and many, such as resource availability, vary substantially through time. Therefore identifying differences between limiting factors may prove to be beyond the scope of what is possible at this stage,

but it is useful to examine the limited available data. For example, one important observation is that Flaming Gorge Reservoir is deep, so likely provides abundant and stable cold water, while Boysen Reservoir is quite shallow given its area, and experiences warmer air temperatures. Warming has been linked to burbot declines in the southern extent of their distribution. Studies in Oneida Lake, New York found a high occurrence of empty stomachs and reduced liver energy density during warm summers, suggesting high summer temperatures may be especially concerning (Holker et al. 2004; Jackson et al. 2008). The Wind River Drainage is already at the southern extent of native burbot distribution and the Green River Drainage is even further south, but dam construction has substantially altered the thermal regime of the Green River creating reservoir and tailwater habitat suitable for burbot (Gardunio et al. 2011). Flaming Gorge Reservoir reaches a maximum depth of 133 m likely creating plenty of cold-water habitat. In fact, the shallower lakes/reservoirs in the Wind River drainage (Table 2) may be more affected by warming.

"Disturbance" is another hypothesis associated with introduction success (Havel et al. 2005; Hierro et al. 2006), and may, in part, be leading to the success of introduced burbot in the Green River drainage. It could be interacting with the "empty niche" hypothesis which suggests that if the invaded community is unsaturated the invader can occupy an unused niche and utilize spare resources (Catford et al. 2009; Hierro et al. 2005). Reservoirs, a novel and man-made habitat, are relatively young and often contain a mélange of species, some of which have not evolved together. As a result there may be more under-utilized resources. It is possible that no fish species is able to fully occupy or defend available habitat in a reservoir as well as native fish species occurring in naturally available habitat. Both the Flaming Gorge and Fontenelle reservoirs host a limited fish assemblage and many are non-native (>60%). This high proportion of non-native species may be indicative of a more disturbed habitat and greater food web instability, as has been suggested generally for reservoir habitats (Havel et al. 2005). However, the higher proportion of non-natives could also reflect the lower native species richness of the Green River Drainage.

The most likely explanation for the success of Green River burbot is a combination of burbot traits and the environment. The "habitat filtering" hypothesis suggests that burbot will be successful if they are adapted to the environmental conditions of the introduced system (Fausch 2008; Melbourne et al. 2007). Flaming Gorge and Fontenelle reservoirs are large deep reservoirs which likely provide a good environmental match for burbot. Fish require good feeding, spawning, and refugia habitat (Schlosser and Angermeier 1995), and these are all present. These reservoirs have a high availability of forage fish and crayfish, ample spawning habitat, and good refugia habitat, including rocky slopes with good cover and cold water refuges (unpublished data).

Habitat quality and habitat loss are thought to be major factors in burbot declines in their native range, with dams being especially detrimental for riverine populations (Stapanian et al. 2010). However, the damming of the Green River has likely been an important factor facilitating introduction success in the Green River by creating "niche opportunities", primarily cooler, more lentic environments, that are not ideal habitat for native species (Olden et al. 2006). In addition, reservoir habitat often experiences higher levels of physical disturbance that can facilitate introduction success (Havel et al. 2005).

There are numerous aquatic species where introduced and native populations are relatively widespread. However, few comparisons have been made of population demographics or fish habitat relationships between these native and introduced populations. Too often monitoring will focus on the invaded population without thought of the native population. An effective comparison requires comparable data for both populations. Our comparison would have been improved if better data on population demography (e.g., age and growth), resource availability, and important environmental factors such as temperature had existed. However, comparing native and nonnative populations, especially when they are in close geographic proximity, is potentially a powerful approach for determining factors driving introduction success and identifying factors limiting native populations. Our comparison suggests the lack of cold, deep habitat in the Wind River drainage could be limiting for burbot populations. This will potentially make these populations highly susceptible to climate change. By understanding factors driving introduction success, it might be possible to more effectively manage introduced species, while simultaneously protecting populations in their native range.

Acknowledgements

References

Abrahamse MS (2008) Abundance and structure of burbot *Lota lota* population in lakes and reservoirs of the Wind River drainage, Wyoming. MS Thesis, University of Wyoming, 138 pp

Anderson RO, Neumann RM (1996) Length, weight, and associated structural indices. In: Murphy BR, Willis DW (eds) Fisheries Techniques. 2nd edn. American Fisheries Society, Bethesda, Maryland, pp 447–482

Blossey B, Notzold R (1995) Evolution of increased competitvie ability in invasive nonindigenous plants - a hypothesis. *Journal of Ecology* 83:887–889, https://doi.org/10.2307/2261425

Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144: 1–11, https://doi.org/10.1007/s00442-005-0070-z

Budy P, Thiede GP, Lobón-Cerviá J, Fernandez GG, McHugh P, McIntosh A, Vøllestad LA, Becares E, Jellyman P (2013) Limitation and facilitation of one of the world's most invasive fish: an intercontinental comparison. *Ecology* 94: 356–367, https://doi.org/10.1890/12-0628.1

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22–40, https://doi.org/10.1111/j.1472-4642.2008.00521.x

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions* 8: 1023–1037, https://doi.org/10.1007/s10530-005-3735-y

Fausch KD (2008) A paradox of trout invasions in North America. *Biological Invasions* 10: 685–701, https://doi.org/10.1007/s10530-007-9162-5

Fisher SJ, Willis DW, Pope KL (1996) An assessment of burbot (*Lota lota*) weight-length data from North American populations. *Canadian Journal of Zoology* 74: 570–575, https://doi.org/10.1139/z96-063

Gardunio EI, Myrick CA, Ridenour RA, Keith RM, Amadio CJ (2011) Invasion of illegally introduced burbot in the upper Colorado River Basin, USA. *Journal of Applied Ichthyology* 27: 36–42 , https://doi.org/10.1111/j.1439-0426.2011.01841.x

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14: 407–418, https://doi.org/10.1111/j.1461-0248.2011.01594.x

Havel JE, Lee CE, Vander Zanden MJ (2005) Do reservoirs facilitate invasions into landscapes? *Bioscience* 55: 518–525, https://doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2.0.CO;2

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93: 5–15, https://doi.org/10.1111/j.0022-0477.2004.00953.x

Hierro JL, Villarreal D, Eren O, Graham JM, Callaway RM (2006) Disturbance facilitates invasion: the effects are stronger abroad than at home. *American Naturalist* 168: 144–156, https://doi.org/10.1086/505767

Hofmann N, Fischer P (2002) Temperature preferences and critical thermal limits of burbot: implications for habitat selection and ontogenetic habtiat shift. *Transactions of the American Fisheries Society* 131: 1164–1172, https://doi.org/10.1577/1548-8659(2002)131<1164:TPACTL>2.0.CO;2

Holker F, Volmann S, Wolter C, LM van Dijk P, Hardewig I (2004) Colonization of the freshwater environment by a marine invader: how to cope with warm summer temperatures. *Evolutionary Ecology Research* 6: 1123–1144

Hubert WA, Dufek D, Deromedi J, Johnson K, Roth S, Skates D (2008) Burbot in the Wind River drainage of Wyoming: knowledge of stocks and management issues. *American Fisheries Society Symposium* 59: 187–199

Jackson JR, VanDeValk AJ, Forney JL, Lantry BF, Brooking TE, Rudstam LG (2008) Long-term trends in burbot abundance in Oneida Lake, New York: life at the southern edge of the range in an era of climate change. *American Fisheries Society Symposium* 59: 131–152

Jacobs GR, Madenjian CP, Bunnell DB, Holuszko JD (2010) Diet of lake trout and burbot in Northern Lake Michigan during spring: evidence of ecological interaction. *Journal of Great Lakes Research* 36: 312–317, https://doi.org/10.1016/j.jglr.2010.02.007

Klobucar SL, Saunders WC, Budy P (2016) A *Lota lota* consumption: trophic dynamics of non-native burbot in a valuable sport fishery. *Transactions of the American Fisheries Society* 145: 1386–1398, https://doi.org/10.1080/00028487.2016.1227372

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2: 286–293, https://doi.org/10.1046/j.1461-0248.1999.00083.x

Krueger KL, Hubert WA (1997) Assessment of lentic burbot populations in the Big Horn Wind River drainage, Wyoming. *Journal of Freshwater Ecology* 12: 453–463, https://doi.org/10.1080/02705060.1997.9663556

Kulhanek SA, Ricciardi A, Leung B (2011) Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? *Ecological Applications* 21: 189–202, https://doi.org/10.1890/09-1452.1

Lewandowski S (2015) Exploitation of burbot *Lota lota* in the Wind River drainage, Wyoming. Montana State University, 51 pp

Livingstone DM, Lotter AF (1998) The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology* 19: 181–198 , https://doi.org/10.1023/A:1007904817619

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution* 3: 182–196, https://doi.org/10.1002/ece3.431

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710, https://doi.org/10.2307/2641039

Mandeville E, Parchman TL, McDonald DB, Buerkle C (2015) Highly variable reproductive isolation among pairs of *Catostomus* species. *Molecular Ecology* 24: 1856–1872, https://doi.org/10.1111/mec.13118

Marschall EA, Crowder LB (1996) Assessing population responses to multiple anthropogenic effects: a case study with brook trout. *Ecological Applications* 6: 152–167, https://doi.org/10.2307/2269561

McPhail JD, Paragamian VL (2000) Burbot biology and life history. In: Paragamian VL, Willis DW (eds), Burbot: biology, ecology, and management. Fisheries Management Section Publication 1. American Fisheries Society, Spokane, Washington, pp 11–23

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* 10: 77–94, https://doi.org/10.1111/j.1461-0248.2006.00987.x

Olden JD, Poff NL, Bestgen KR (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* 76: 25–40, https://doi.org/10.1890/05-0330

Paakkonen JPJ, Tikkanen O, Karjalainen J (2003) Development and validation of a bioenergetics model for juvenile and adult burbot. *Journal of Fish Biology* 63: 956–969, https://doi.org/10.1046/j.1095-8649.2003.00203.x

Parchman TL, Gompert Z, Mudge J, Schilkey F, Benkman C, Buerkle C (2012) Genome wide association genetics of an adaptive trait in lodgepole pine. *Molecular Ecology* 21: 2991–3005, https://doi.org/10.1111/j.1365-294X.2012.05513.x

Peterson DP, Fausch KD, White GC (2004) Population ecology of an invasion: effects of brook trout on native cutthroat trout. *Ecological Applications* 14: 754–772, https://doi.org/10.1890/02-5395

Pickrell J, Pritchard J (2012) Inference of population spilts and mixtures from genome-wide allele frequency data. *PloS Genetics* 8: e1002967, https://doi.org/10.1371/journal.pgen.1002967

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-118, http://CRAN.R-project.org/package=nlme

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Renne IJ, Tracy BF, Colonna IA (2006) Shifts in grassland invasibility: effects of soil resources, disturbance, composition, and invader size. *Ecology* 87: 2264–2277, https://doi.org/10.1890/0012-9658(2006)87[2264:SIGIEO]2.0.CO;2

Ruesink JL (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology* 19: 1883–1893 , https://doi.org/10.1111/j.1523-1739.2005.00289.x

Schlosser IJ, Angermeier PL (1995) Spatial variation in demographic processes of litic fishers: conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium* 17: 392–401

Sher AA, Hyatt LA (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biological Invasions* 1: 107–114, https://doi.org/10.1023/A:1010050420466

Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81: 3074–3086, https://doi.org/10.1890/0012-9658(2000)081[3074:DLIRAT]2.0.CO;2

Simon JR (1951) Wyoming fishes. Wyoming Game and Fish Department, Cheyenne, Wyoming, 129 pp

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology* 83: 2575–2590, https://doi.org/10.1890/0012-9658(2002)083[2575:BIRAME]2.0.CO;2

Stapanian MA, Paragamian VL, Madenjian CP, Jackson JR, Lappalainen J, Evenson MJ, Neufeld MD (2010) Worldwide status of burbot and conservation measures. *Fish and Fisheries* 11: 34–56, https://doi.org/10.1111/j.1467-2979.2009.00340.x

Stranko SA, Hilderbrand RH, Morgan II RP, Staley MW, Becker AJ, Roseberry-Lincoln A, Perry ES, Jacobson PT (2008) Brook trout declines with land cover and temperature changes in Maryland. *North American Journal of Fisheries Management* 28: 1223–1232, https://doi.org/10.1577/M07-032.1

Underwood ZE (2015) The movements and population structure of burbot (*Lota lota*) in the Wind River, Wyoming. MS Thesis, University of Wyoming, 78 pp

Underwood ZE, Mandeville EG, Walters AW (2016) Population connectivity and genetic structure of burbot (*Lota lota*) populations in the Wind River Basin, Wyoming. *Hydrobiologia* 765: 329–342 , https://doi.org/10.1007/s10750-015-2422-y

Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion - new questions from old patterns. *Oikos* 74: 159–164, https://doi.org/10.2307/3545686

Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity and Distributions* 14: 569–580, https://doi.org/10.1111/j.1472-4642.2008.00473.x

Supplementary material

The following supplementary material is available for this article:

Table S1. Fish species presence in lakes and reservoirs inhabited by burbot in the introduced Green River (Fontenelle and Flaming Gorge reservoirs) and native Wind River (Boysen Reservoir and Bull, Lower Dinwoody, Ring, Trail, Torrey, and Upper Dinwoody lakes) drainages, Wyoming.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2017/Supplements/AI_2017_Walters_etal_TableS1.xls