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A *Lota lota* consumption: trophic dynamics of non-native Burbot in a valuable sport fishery

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<A>Abstract

In managed sport fisheries, unintentional and illegal introductions of species disrupt food webs and threaten the success of these fisheries. While many populations of Burbot *Lota lota* are declining in their native range, a non-native population recently expanded into Flaming Gorge Reservoir, Wyoming-Utah, and threatens to disrupt predator-prey interactions within this popular sport fishery. To determine potential impacts on sport fishes, especially trophy Lake Trout *Salvelinus namaycush*, we assessed the relative abundance of Burbot and quantified potential trophic or food web impacts of this population using diet, stable isotope and bioenergetic analyses. While we did not detect significant potential for competition between Burbot and Lake Trout for food resources (Schoener's index; $\alpha = 0.13$), overall consumption by Burbot likely affects other sport fishes as indicated by our analyses of trophic niche space. Our diet analyses suggest that crayfish are important diet items across time (89.3% and 49.4% by weight in autumn and winter) and size classes (77.5%, 76.6%, 39.7% by weight for small, medium, and large Burbot). However, overall consumption by Burbot increases as water temperatures cool, and fish consumption increased during winter. Specifically, large Burbot consume more salmonids and we estimated (bioenergetically) up to 70% of growth occurs in late autumn and winter. Further, our population-wide consumption estimates indicated that Burbot could consume up to double the biomass of Rainbow Trout *Oncorhynchus mykiss* stocked annually ($> 1.3 \cdot 10^5$ kg; > 1 million individuals) in Flaming Gorge Reservoir. Overall, we provide some of the first information regarding trophic interactions of Burbot outside of their native range, and these findings can help inform the management of sport fisheries should Burbot range expansion occur elsewhere.

<A>Introduction

Non-native species continue to be a foremost threat to conservation and management globally, and freshwater ecosystems are among the most highly altered by invasive species (Mooney and Hobbs 2000, Marchetti et al. 2004a). Anthropogenic assisted introductions, both intentional and unintentional, legal and illegal, have led to the proliferation of non-native fishes across the United States (Rahel 2000, 2004). Accordingly, while some fishes are experiencing declines in their native range, introductions and subsequent range expansions allow for potentially more successful populations relative to the native ranges (e.g., Brook Trout *Salvelinus fontinalis*; Peterson et al. 2004; Hudy et al. 2008). Thus, regardless of introduction pathway, introduced fishes can potentially prove detrimental to ecological and economic underpinnings of successful fisheries (Dunham et al. 2004; Gozlan et al. 2010).

Widespread stocking programs that include non-native fishes support valuable sport fisheries, and managers are tasked with creating a balance between angler satisfaction and food web dynamics (Eby et al. 2006). Lake Michigan, where Burbot *Lota lota* are native, provides a classic example of the many complexities associated fish introductions resulting from attempts to achieve this balance; a struggle that began in the early 20th century and continues today (Stewart et al. 1981; Tsehaye et al. 2014). Here, the balance of an invasive prey base (e.g., Rainbow Smelt *Osmerus mordax* and Alewife *Alosa pseudoarengus*) and predators including native (e.g., Lake Trout *Salvelinus namaycush*) and non-native (e.g., Chinook Salmon *Oncorhyncus tshawytscha*) salmonids have become destabilized on a number of occasions due to disproportionate stocking densities and non-native species introductions.

Across the western United States, stocked sport fisheries are especially prevalent in numerous man-made reservoirs, and often included stocked top predators (Moyle and Marchetti

2006). In accordance with the unnatural characteristic of reservoirs, stocked fishes often create a mixed assemblage of native and non-native sport fishes, with almost entire non-native assemblages relatively common (Martinez et al. 1994; Clarkson et al. 2005). Often times, these mixed assemblages require annual stocking of predators, which can decouple the balance of predator consumption demand and prey availability as seen in Lake Michigan (Johnson and Martinez 2000).

Reservoirs represent novel habitats for both native (e.g., creating standing water in naturally flowing river systems) and non-native species alike, creating sport fisheries that can be relatively harmless to native fishes and highly popular among anglers for stocked non-native fishes (Marchetti et al. 2004b; Johnson et al. 2009; but see Rubidge and Taylor 2005). However, when unauthorized introductions occur, managers are confronted with uncertainty toward food web dynamics and overall ecosystem stability in these highly managed fisheries (Leung et al. 2002, Maguire 2004). In the face of this uncertainty, management can be difficult and further complicated with balancing ecological, social, and economic concerns (Quist and Hubert 2004).

In the upper Colorado River Basin, many reservoirs fragment the region, but also create valuable sport fisheries as a result (Dibble et al. 2015). Prized sport fish in these reservoirs are often non-native salmonids. However, illegal introductions of other fishes have led to many populations of cool- and warm-water fishes across the basin, which pose threats to actively managed species (Johnson et al. 2009). Flaming Gorge Reservoir (FGR), WY-UT, one of the largest reservoirs and most popular fisheries in the upper Colorado River Basin, is threatened by a relatively recent Burbot introduction and expansion. Within FGR, angling opportunities are abundant for trophy Lake Trout, which are primarily supported by a Kokanee Salmon

Oncorhynchus nerka population that is popular among anglers. Additionally, Rainbow Trout *Oncorhynchus mykiss* and Smallmouth Bass *Micropterus dolomieu* provide further angling opportunities. While these sport fishes are also non-native, they are actively and intentionally managed within FGR.

In the early 2000s, Burbot began to expand downstream in the Green River drainage of the upper Colorado River Basin from Big Sandy Reservoir, WY, where Burbot were established from illegal introductions in the 1990s (Garduino et al. 2011). By 2006, Burbot were established in FGR. Burbot, demonstrated to be voracious predators in their native range, could pose a threat to highly valued fisheries within FGR through direct and indirect competition (Rudstam et al. 1995; Jacobs et al. 2010). Unlike the Lake Trout and Kokanee Salmon populations that FGR is noted for, Burbot can inhabit both lotic and lentic waters. As such, Burbot pose a threat for further expansion throughout the basin and managers fear their expansion will be detrimental to the sport fish of FGR. As a Holarctic, circumpolar species, Burbot are relatively well studied in their native ranges throughout Asia, Europe, and North America; however, many native populations have experienced dramatic declines (Stapanian et al. 2010), and very little is known about Burbot in non-native ranges (but see Klein et al. 2015). While niche partitioning between Burbot and fishes in their native range has been explored (e.g., Guzzo et al. 2015), we require an understanding of trophic dynamics that have contributed to their success in their non-native range, especially as nearby native populations are in decline (e.g., Krueger and Hubert 1997).

In this study, we investigated the population status of Burbot in FGR, and assessed potential direct and indirect impacts of Burbot on valued sport fish, with a primary focus on trophy Lake Trout. We collected diet and stable isotope samples, and extended our findings using a bioenergetics model to quantify predation potential and competition. Collectively, we used these data to show how a newly established population of Burbot, across a range of population densities, could affect highly managed sport fisheries, especially where annual stocking promotes angler success. Our findings demonstrate that efficient predators such as Burbot can consume many stocked sport fishes (e.g., Rainbow Trout) as well as important prey resources (e.g., crayfish) for these sport fishes. If Burbot expansion continues to other waterbodies, our study provides a baseline to better understand and manage the fishery.

<A>Methods

Study site.—

Flaming Gorge Reservoir, created by the impoundment of the Green River in 1962, lies on the border of northeast Utah and southwest Wyoming (Figure 1). At capacity, FGR is approximately 145 km long, encompasses 17,000 ha of water, and has a mean depth of 34 m. Previous studies (e.g., Yule and Luecke 1993) separated the reservoir into three distinct regions based on physical and chemical characteristics: 1) the Canyon region—a narrow and deep (maximum depth = 134m), stratified, nearly oligotrophic region extending approximately 38 km north of the dam; 2) the Open Hills region—a wider, wind-blown stretch of moderately deep (maximum depth= 61m) water classified as mesotrophic which extends 48 km north of the Canyon region; and, 3) the Inflow region—a relatively shallow (maximum depth = 24 m), often turbid region that receives water from the Green and Blacks Fork rivers and extends 32 km above the Open Hills region. Few Burbot are found in the Canyon region, thus, we excluded those samples from our analyses in this study.

Currently, all sportfish in FGR are introduced. Lake Trout and Smallmouth Bass are self-sustaining, while Kokanee Salmon and Rainbow Trout populations are supplemented by annual stocking. Northern Crayfish *Orconectes virilis* are abundant and an important food resources for bass and trout. Additional sport fish in the reservoir include Brown Trout *Salmo trutta*, Cutthroat Trout *Onchorhynchus clarkii*, and Channel Catfish *Ictalurus punctanus*. Non-game fishes include White Sucker *Catostomus commersonii*, Utah Chub *Gila atraria*, Common Carp *Cyprinus carpio*, Redside Shiner *Richadsonius balteatus*, and Flannelmouth Sucker *Catostomus latipinnis*. Only the Flannelmouth Sucker is native to the basin and is listed as a species of concern. For anglers, Burbot are under a catch and kill regulation in FGR (both states).

Burbot catch and diet collection.—

To assess population trend, diet composition, and total consumption by Burbot and Lake Trout in FGR, we sampled fishes during two distinct seasons, autumn 2012 and winter 2013. Autumn sampling occurred during 24 October – 15 November, 2012 and winter sampling occurred during 15 January – 22 February, 2013. During autumn, we used multi-filament trammel nets (33m long by 1.5m tall; internal mesh= 20mm, external mesh=100mm) set in the littoral zone (5-25m) to collect fish. We set nets at established sampling sites in the Inflow and Open Hills regions of the reservoir. Nets were set at dusk and fished overnight (approximately 1700-0900 hrs). Additionally, in conjunction with our sampling, we used data from long-term autumn trammel net sampling (since 2006, Wyoming Department of Game and Fish and Utah Division of Wildlife Resources (UDWR), unpublished data), to estimate population growth rate. We estimated population growth rate (λ) based on the trend in corrected CPUE using a log-linear regression-based trend model (Dennis and Taper 1994; Morris and Doak 2002). This analysis provides support to better understand how population trend (e.g., population declining, stable, or increasing) might affect reservoir wide consumption estimates.

During winter sampling, we collected fish through the ice using hook-and-line sampling, and targeted Burbot in the evening (approximately 1700-0200 hrs). Winter sampling occurred at or near sites sampled during autumn in the Inflow and Open Hills regions. We targeted large Lake Trout (> 500 mm) during the day in the Open Hills region (approximately 0900-1600 hrs), which we hypothesized would be the region large Lake Trout and Burbot are most likely to overlap.

We identified, weighed (g), and measured (total length, TL; mm) all fish. To gather diets and stable isotopes, we sacrificed all Burbot and a subset of Lake Trout (≤ 600 mm TL, including all mortalities, n = 26). In the field, we placed stomachs in 95% ethanol for later processing. We performed gastric lavage on large Lake Trout captured via hook-and-line (≥ 600 mm TL, n = 11). All non-target species were released.

Diet analysis.—

To characterize fish diet and selectivity, we identified prey items to the lowest taxon possible and divided prey into representative categories (crayfish, fish, other). When possible, we further divided these general categories (e.g., ‘fish’ by species, ‘other’ by group), measured percent wet weight of each prey category for each individual fish, and then calculated diet proportion and occurrence relative to the total sample size. We weighed prey fish individually. For zooplankton and invertebrate prey, we weighed each taxonomic group en masse to the nearest 0.001 g blot-dry wet weight. To estimate total consumption (g), we subtracted empty stomach weight from full stomach weight, or summed the weight of all prey items (e.g., diets obtained via gastric lavage). We analyzed Burbot diets for temporal (autumn vs. winter) and size class (<400 mm = small, 400-650 mm = medium, and >650 mm = large) variability. Due to lower sample size, we analyzed Lake Trout diets by size class, but pooled across season and site. To determine potential interspecific competition between Burbot and Lake Trout, we calculated diet overlap using Schoener's index, α (Schoener 1970):

$$\alpha = 1 - 0.5 \cdot \left(\sum_{i=1}^{n} \left|p_{xi} - p_{yi}\right|\right),$$

where *i* is a given prey item, *p* is the proportion of *i*, and *x* and *y* are Burbot and Lake Trout. The single value α is diet overlap from 0 (no overlap) to 1 (complete overlap), and values greater than 0.6 are indicative of significant diet overlap (Schoener 1970).

Stable isotopes.—

We used carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes to further explore a time-integrated representation of Burbot diets and potential for competition with other sport fishes in FGR. For stable isotope analyses, we used dorsal muscle tissue and dorsal fin clips from fish predators (small Burbot n = 15, medium Burbot n = 25, large Burbot n = 6, Lake Trout n = 29, Rainbow Trout n = 12, Smallmouth Bass n = 4, and Kokanee Salmon n = 2). Samples were dried for 48 hrs at 70°C, ground into a homogenized powder, and placed into pre-weighed tin capsules. Fish tissues samples were processed at the Washington State University Stable Isotope Core laboratory for analysis of $\delta^{13}C$ and $\delta^{15}N$, and percent composition of both carbon and nitrogen. Isotopic signatures are reported in δ-notation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \cdot 1000 ,$$

where R_{sample} is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ found in the tissue or filter sample, and $R_{standard}$ is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ found in the standard sample. The standard for $\delta^{13}C$ is PeeDee belemnite and the standard for $\delta^{15}N$ is atmospheric nitrogen.

To calculate trophic position of Burbot and other sport fishes in FGR, we used:

$$TP_i = \left(\frac{\delta^{15}N_i - \delta^{15}N_{baseline}}{3.4}\right) + 1,$$

where TP_i is the trophic position of species i, N_i is the nitrogen signature of species i, and $N_{baseline}$ is the nitrogen signature for primary producers (Vander Zanden & Rasmussen 1999). We assumed that primary producers have a trophic position of 1 and a $\delta^{15}N$ trophic fractionation value of 3.4 ± 1.1‰ (Minagama & Wada 1984). We used an average value of macrophytes and phytoplankton to represent primary producers ($\delta^{15}N = 9.36$ ‰; Luecke and Mears 2011).

To evaluate characteristics trophic overlap of Burbot with other sport fishes, we used SIBER (Stable Isotope Bayesian Ellipses) in R, which uses Bayesian inference techniques to describe niche and community metrics (Jackson et al. 2011). The SIBER model uses bivariate δ13C and δ15N data to represent isotopic trophic niche space for a species or group. The SIBER model produces ellipses around the centroid that include ± 1 SD. We calculated the percent species overlap at the intersection of ellipse areas. Kokanee Salmon were not included in this analysis owing to low sample size; however, our initial plots showed no potential overlap.

Bioenergetics.—

We modified equations from Bioenergetics 3.0 (Hanson et al. 1997) to run in R version 3.2.1 (R Development Core Team, 2015) to estimate annual Burbot consumption (kg; Kitchell et al. 1977). We used physiological parameters from Rudstam et al. (1995). To estimate reservoir-wide annual consumption by Burbot, we first estimated size-specific annual consumption based on individual Burbot, and then applied these estimates to an age structure and abundance index of Burbot within FGR. First, annual growth (mm) was approximated using the difference between modes from a length-frequency histogram of our 2012 – 2013 catch, and we determined mean length at age for each year class from 1000 randomly drawn lengths from normally distributed Burbot lengths for estimated year classes. We corroborated these growth estimates using otoliths and mark-recapture information from Burbot tagged during 2011 – 2016 (UDWR, unpublished data). Mark-recapture data is derived from annual UDWR Burbot fishing derbies, in which ‘prize fish’ are tagged and released for a given year’s tournament, but often caught during subsequent years (1 – 4 years growth; n = 37, length at first capture = 279 – 731 mm TL). These data provide accurate estimates of yearly growth, which we used to corroborate length-frequency modes. We applied age-3 to our smallest size class sampled, and our largest fish were grouped to a size class of age-10+. Otoliths confirmed that our sampling methods captured burbot age-3 and older (Luecke and Mears 2011), and our length-frequencies modes appropriately fit the FGR Burbot population. We then fit a von Bertalanffy growth model (Ricker 1975) for final length-at-age predictions:

$$burbot\ length = 1065.58 \cdot (1 - e^{-(0.13 \cdot (burbot\ age - 0.16))}),$$

To obtain an appropriate growth input for bioenergetics (annual change in weight, g), we developed a length-weight relationship for Burbot caught in FGR during 2012-2013 (*n* = 318) and applied the above length-at-age model, where the power transformed length-weight relationship yielded:

$$burbot\ weight = e^{-12.32 + 3.02 \cdot log_e(burbot\ length)},$$

For bioenergetic analyses, we combined Burbot diet proportions (% wet weight, g), as described above, by length (e.g., < 400, 400 – 650, > 650 mm) and season (e.g., fall, winter). We used temperature profiles (early May to early December; 2009 – 2015; UDWR, unpublished data) in bi-weekly periods averaged across years to obtain a ‘typical’ thermal experience for Burbot and extrapolated water temperatures for dates in between. Between December 15 and March 15, we assumed the reservoir was ice covered or completely mixed at or below 4°C. Throughout the remained of the year, we assumed Burbot behaviorally thermoregulated to live at the optimal temperature for gadoids (13.7°C; Rudstam et al. 1995, but see Harrison et al. 2016). When optimal temperature was not available in the water column, we assumed Burbot would occupy the temperature nearest to 13.7°C (e.g., 4°C from December 15 – March 15).

As a coarse index of relative Burbot abundance and density in FGR, we applied the Schumacher and Eschmeyer method (Krebs 1999) using mark-recapture of tagged Burbot (UDWR, unpublished data). While we acknowledge we violated some assumptions of this method, confounding factors (e.g., catch and kill regulation) limited our overall ability to use a more robust method. Nonetheless, our index of abundance (mean = 140,000 individuals; range = 80,000 – 510,000 individuals; 95% CI) provides density estimates similar to other studies where Burbot are successful in their native range (e.g., Parker et al. 1989; Rudstam et al. 1995). Further, this estimate provides us a relative measure of the potential impact of the total population (e.g., a low and high estimate). To estimate annual consumption across the reservoir, we multiplied bioenergetic estimates of consumption for the mean length fish for each age class (3 – 10+ years old) by the proportion of sampled Burbot in each age class and by the range of total population estimates. Due to smaller sample size and growth approaching the asymptote of our von Bertalanffy growth model, we pooled fish age 10 and greater to a single age category (e.g., Madenjian et al. 2011)

<A>Results

<B>Burbot Catch and Diets

The Wyoming Department of Game and Fish and Utah Division of Wildlife Resources have monitored the fall distribution and abundance of Burbot in FGR since 2006, following similar trammel netting methods as described above. Overall, catch per unit effort is variable, but our analyses demonstrate a relatively stable population across the Inflow and Open Hills regions (λ_{Inflow} = 1.10, 95% CI = 0.71 – 1.69; $\lambda_{\text{Open Hills}}$ = 1.06, 95% CI = 0.79 – 1.42).

We examined stomach contents from 385 Burbot (518 mm ± 5.8 [mean TL ± 1 SE]; range = 307 – 850 mm) collected during autumn 2012 (n = 188) and winter 2013 (n = 197). Of these, 307 stomachs contained diet items, while 78 were empty; we excluded empty stomachs from further diet analyses. Of the Burbot stomachs that contained prey items, Northern Crayfish (81.4 % by occurrence) were most often consumed, followed by fish (40.1 % by occurrence; Table 1). However, we noted variation in diet composition and consumption across time and size classes.

We analyzed diets from 78 % of Burbot captured in autumn (n = 147) and 81% of Burbot captured in winter (n = 160). Total mean consumption by Burbot was significantly greater ($t_{(\text{DF} = 189)} = 3.70$, $P < 0.01$) in winter than during autumn (Table 1; 26.2 ± 3.9 vs. 11.3 ± 1.2 g [mean ± 1 SE]); however, mean length of Burbot captured in winter was also greater than in autumn. During autumn, Burbot most often consumed crayfish (89.3% by weight) and some fish (7.8% by weight). In winter, Burbot consumption of crayfish (49.4% by weight) was considerably less than autumn, and similar to consumption of fishes during winter (47.8% by weight). Consumption of fish was more than six-fold greater during winter relative to autumn.

Prey fish composition in Burbot diets, and total consumption of fishes, also varied by season (Table 1). During autumn, of fish consumed, Burbot primarily consumed forage fishes (e.g., sucker and chub spp.; 68.6% by weight). We observed no consumption of salmonids, and the only sport fish we identified in autumn diets was Smallmouth Bass (5.6% by weight). However, during winter salmonids composed the greatest proportion of fish in Burbot diets (71.7% by weight). Burbot still consumed forage fishes, but in lesser proportion than autumn (11.9% by weight). Of the salmonids consumed during the winter, Rainbow Trout (60.5% by weight) and Lake Trout (31.1% by weight) made up the majority of salmonids consumed. Overall, cannibalism was approximately three times more common in winter than autumn (17.9 % vs 5.7 % occurrence) but made up a greater proportion of the total diet in autumn (22.7% vs. 8.6% by weight).

When compared across size classes, small (< 400 mm; n = 37) and medium (400 – 650 mm; n = 225) Burbot exhibited similar feeding patterns; however, diet composition and consumption of large Burbot (> 650 mm; n = 45) was significantly different from these size classes (Table 1; Figure 2a). Small and medium sized Burbot consumed similar proportions of crayfish (77.5% and 76.6% by weight), and ate fishes in similar proportions (18.3% and 20.1% by weight). Large Burbot were primarily piscivorous (57.9% by weight), but also consumed about 40% crayfish. Total consumption increased significantly with size class. Large Burbot consumed the greatest prey biomass (52.5 g ± 10.0 [mean ± 1 SE]), while medium (13.5 g ± 1.2) and small Burbot (4.1 g ± 0.7) consumed significantly less ($F_{(2, 304)} = 36.1$, $P < 0.001$). When consuming fish, small Burbot most often consumed Smallmouth Bass (51.5% by weight) and forage fishes (20.4% by weight). Small Burbot consumed no salmonids. Medium Burbot consumed salmonids (32.5% by weight), forage fishes (26.8% by weight), and Smallmouth Bass

(21.5% by weight) with similar frequency. In contrast, large Burbot predominately consumed salmonids (86% by weight), while forage fishes comprised the only other significant fish prey (9.0% by weight). Of the salmonids consumed, most were Rainbow Trout (67.8% by weight) and Lake Trout (22.6% by weight), and this pattern was similar for salmonids consumed by medium Burbot (59.7% and 17.5% by weight, respectively).

<B>Lake Trout Catch and Diets

We analyzed a total of 37 Lake Trout diets from trammel net and hook-and-line sampling in autumn and winter 2012-2013 (Table 2). Small Lake Trout (<400 mm; n = 9) consumed mostly zooplankton (76.5% by weight) and few fish (23.5% by weight), medium-sized Lake Trout (400-650 mm; n = 17) consumed mostly fish (84.0% by weight) and few crayfish (11.0% by weight; Figure 2b). When consuming fishes, small and medium-sized Lake Trout almost entirely consumed forage fishes (95.2% by weight). Large, trophy Lake Trout (>650 mm, mean TL = 883.6 ± 42.4 mm; n = 11) consumed fish exclusively (100% by weight), and mean total consumption by large Lake Trout was much greater than large Burbot (212.1 ± 63.24 vs. 52.5 ± 10.0 g) These large Lake Trout consumed almost entirely other salmonids (>99.9% by weight), with most of these salmonids being Kokanee Salmon (83.8% by count). We did not observe consumption of Burbot by Lake Trout.

<B>Potential Competition and Bioenergetics

Based Schoener's index, we observed no potential for interspecific competition, and very little overall diet overlap, between Burbot (all sizes pooled) and Lake Trout (all sizes pooled; α = 0.13). We also observed very little overlap when comparing small, medium, and large Burbot separately to all Lake Trout (α = 0.01, 0.06, and 0.19, respectively). This notion matches our diet analyses; large Lake Trout consumed mostly Kokanee Salmon, while Kokanee Salmon accounted for less than 3% of salmonids consumed by large Burbot (Tables 1, 2). δ^{15}N signatures and thus, trophic positions, of small (TP = 2.16 ± 0.07 [mean ± 1 SE]), medium (TP = 2.63 ± 0.26 [mean ± 1 SE]), and large Burbot (TP = 2.99 ± 0.07 [mean ± 1 SE]), were significantly different ($F_{(2,43)}$ = 15.7, P < 0.005), and δ^{13}C signatures indicated Burbot may compete more with littoral Rainbow Trout and Smallmouth Bass than pelagic Lake Trout (Figure 3). Large Lake Trout trophic position (TP = 3.24 ± 0.06 [mean ± 1 SE]) was significantly greater than that of large Burbot ($t_{(189)}$ = 2.63, P = 0.02). Rainbow Trout trophic position (TP = 2.22 ± 0.38 [mean ± 1 SE]) was similar to small Burbot (t_{19} = 0.43, p = 0.67), and Smallmouth Bass trophic position (TP = 2.49 ± 0.07 [mean ± 1 SE]) was similar to medium Burbot (t_{12} = 1.36, P = 0.20). Additionally, our analyses of trophic niche space showed no overlap between Burbot (of any size group) and Lake Trout. However, we did note diet overlap between Burbot and Rainbow Trout, and Burbot and Smallmouth Bass. Specifically, small Burbot and medium Burbot niche space overlapped with 21.8% and 17.9% of Rainbow Trout niche space, and medium Burbot also overlapped with 44% of Smallmouth Bass niche space (see Appendix 1).

Annual consumption by Burbot, on an individual basis, increased with age (1622 – 8318 $g \cdot yr^{-1}$, age-3 – age-10+), and age specific bioenergetic efficiency (proportion of maximum consumption, *BioEff*; Budy et al. 2013) decreased with age, but was relatively high overall

(*BioEff* = 0.57 – 0.69; age-10+ and age-3; see Appendix 2). Overall, at the population level, we estimate that Burbot consumed between $3.3 \cdot 10^5 – 2.4 \cdot 10^6$ kg of prey annually (mean = $5.8 \cdot 10^5$ kg). Crayfish accounted for 84% of annual Burbot consumption, while fish and other prey items accounted for 14% and 2% of annual Burbot consumption (Table 3; Figure 4a). When consuming fishes, 62% of annual Burbot consumption was salmonids (66% Rainbow Trout, 22% Lake Trout, 10% unidentified, and 2% Kokanee Salmon, respectively; Figure 4c) while 17% was forage fishes, 10% other Burbot, 10% Smallmouth Bass, and 1% unidentified. Age-5 Burbot (451 – 524 mm; mean = 490 mm) made up the greatest proportion of the overall population (30%), and also consumed the most prey biomass annually ($1.5 \cdot 10^5$ kg). Age-3 Burbot (307 – 367 mm; mean = 324 mm; 10% of the population) consumed the least prey biomass annually ($2.27 \cdot 10^4$ kg). Age-5 and age-7 (589 – 646 mm; mean = 619 mm) Burbot consumed the most and similar amounts of fish prey annually (1.48 and $1.50 \cdot 10^4$ kg); however, $1.29 \cdot 10^4$ kg of age-7 fish prey was salmonid while only $4.86\ 10^3$ kg was salmonid for age-5 Burbot (Figure 4b).

<A>Discussion

We combined field measurements of Burbot diets from a recently expanded population across seasons and sizes with stable isotope analyses and bioenergetic models to assess the potential for direct and indirect competition with sport fish (e.g., large Lake Trout) in FGR. To better understand and quantify the success of the Burbot expansion into FGR, we extended our bioenergetic predictions to a range of estimated population densities in order to bracket the extent to which a stable Burbot population could affect the food web of this important sport fishery. We observed little evidence that Burbot are competing with Lake Trout for prey resources. However, Burbot are consuming large quantities of fish, including other sport fishes, as well as large quantities of important sport fish prey resources (e.g., crayfish), which could disrupt predator-prey dynamics and the food web within FGR.

Since the expansion of Burbot into FGR, there has been concern and uncertainty about the potential trophic impacts of this novel predator with regard to popular sport fishes. In FGR, the Lake Trout population is popular, long-established and stable, and no longer requires stocking to supplement the fishery. In contrast, the Lake Trout population in Lake Michigan, where Burbot and Lake Trout are both native, has declined as a result of the invasion of other species that lead to the decimation of Lake Trout prey (Rogers et al. 2014; Tsehaye et al. 2014). As such, while these species previously co-existed here in their native range (see also Cott et al. 2011; Guzzo et al. 2016), today Burbot consumption of Lake Trout likely limits rehabilitation efforts in Lake Michigan via direct consumption of an already diminished Lake Trout population (Jacobs et al. 2010). Our results indicate that Burbot and Lake Trout can live in sympatry, in their non-native ranges, especially when prey is not limiting and Lake Trout populations are stable and performing well (e.g., biotic resistance; Fausch 2008). Accordingly, this study and others (e.g., Yule and Luecke 1993) demonstrate Lake Trout feed predominately on Kokanee in FGR, and as such, maintaining a healthy Kokanee population is important for Lake Trout success. On the other hand, Burbot consume other sport fishes, such as Rainbow Trout, in large quantities.

While our study shows that Burbot in FGR primarily consume crayfish, there is potential for direct and indirect competition with other sport fish. From 2006 – 2012, an average of 535,060 (377,906 – 821,121) Rainbow Trout were stocked annually in FGR (UDWR, unpublished data). Assuming these trout are stocked at a catchable size of 200 mm, and weigh approximately 120 g each, an average of 64000 kg of Rainbow Trout are stocked annually. Our bioenergetic analyses indicate the population of Burbot in FGR could consume 29% of these Rainbow Trout at a low Burbot abundance estimate and more than double the biomass of the total Rainbow Trout (> 1 million individuals) stocked annually at the high end of this estimate. Furthermore, competition for food resources between Smallmouth Bass and Burbot could also be substantial, as crayfish are often the primary prey of Smallmouth Bass (Garvey et.al. 2003), and Burbot in FGR could consume more than 117 kg $\cdot$ha^{-1} of crayfish annually.

In their native range, Burbot show the potential to feed opportunistically and outcompete other fishes for desired prey (Knudsen et al. 2010); thus, in non-native waters, the potential for burbot to fill open niche space could contribute to their expansion success (e.g., Vatland and Budy 2007). In FGR, crayfish are relatively abundant and, for benthic predators such as Burbot, relatively easy to capture. On the other hand, because Burbot consume primarily crayfish in FGR, there could be unknown consequences should the crayfish population decline dramatically (e.g., Hein et al. 2007). Conversely, Paragamian (2010) suggests a strong link between Burbot and crayfish in that crayfish abundance increased in Kootenai River following a decline in Burbot. Our bioenergetic analyses suggests high levels of reservoir-wide crayfish consumption, but we have inadequate information on the availability of crayfish across and within years to truly understand how crayfish abundance might control Burbot. However, if crayfish became limited, it is plausible, based on our dietary analyses, that burbot in FGR could shift to other prey (e.g., increased piscivory on sport fish). Cott et al. (2011) demonstrated Burbot can play a role in structuring fish communities with other top predators, and in the Great Lakes, Burbot diets shifted correspondingly as proliferation of new invasive species created abundant new prey (e.g., Round Gobies; Jacobs et al. 2010; Hares et al. 2015). Previous work in FGR demonstrated an increase in juvenile forage fishes following a high water year resulting in increased forage fish recruitment. The following autumn, greater consumption of forage fish was observed, suggesting Burbot opportunistically consumed abundant prey fish (Luecke and Mears 2011). Accordingly, variability in Burbot diets may be due to variability in prey abundance and availability (Pääkkönen 2000); however, in FGR we would need a better understanding of overall prey availability to make better determinations of prey selectivity versus availability.

Across seasons, prey selection could be driven by Burbot life history and/or metabolic demands. Previous work on FGR found that consumption by Burbot increased from summer to autumn (Luecke and Mears 2011); however, in the past, too few winter samples were available to make strong seasonal comparisons. Summer temperatures in the top 10 m of the water column may be too warm for daily vertical migrations to forage, as has been documented in cooler waterbodies of Canada where Burbot are native (Harrison et al. 2013). The increase in consumption from summer to autumn is likely associated with cooling of water temperatures towards the thermal optimum of Burbot, an obligate cold water fish (McPhail and Paragamian 2000). We hypothesize that Burbot consumption further increases in winter, as prey metabolism slows and as they are recovering from winter spawning activities that are energetically costly (Saunders et al. 2014). We also observed increased Burbot cannibalism during winter, which may reflect opportunistic feeding and/or greater intraspecific competition as a result of spawning congregation (Hofmann and Fischer 2001; Cott et al. 2013; Gallagher and Dick 2015)

Our observed differences in Burbot diets and consumption across sizes are likely driven by ontogenetic shifts in behavior. During 2012-2013, small and medium Burbot fed primarily on crayfish prey, while large Burbot were primarily piscivorous. While it is possible small and medium size classes of Burbot may be gape limited; we also observed fish in the diets of Burbot as small as 301 mm, and 11% of Burbot less than 400 mm consumed fish. However, the majority of fish prey consumed by these size classes were bottom and littorally oriented fishes. Small and medium Burbot may avoid feeding in profundal zones to avoid predation themselves and cannibalism, while large Burbot can likely forage more freely and successfully in the littoral with predation fear (Harrison et al. 2013). Overall, the physiological ability of Burbot, across size classes, to consume prey (e.g., gape limitation) corroborates the concept that they are highly effective predators, as has been demonstrated herein and elsewhere (e.g., Kahilainen and Lehtonen 2003). This effective predation may necessarily influence management strategies (e.g., size of fish stocked). As an illustration, in FGR, we observed large Burbot consuming fish greater than 50% of their own total body length. In winter 2013, a 780 mm Burbot consumed an approximately 420 mm Rainbow Trout, more than double average length at stocking, suggesting rainbow trout that overwinter still remain susceptible to predation.

Management Implications.—

Here, we present some of the first data to describe the success and potential impacts of Burbot in their non-native range. Specifically, our study describes potential pathways in which Burbot could affect popular sport fisheries. Overall, there is little evidence for competition between newly established Burbot and long-established Lake Trout, and the lack of trophic overlap suggests they can coexist in novel waterbodies. However, our study indicates that other sport fishes are more likely to be impacted by Burbot. Rainbow Trout and Smallmouth Bass in particular may compete with Burbot for prey, and Burbot consumption of Rainbow Trout could further limit their annual stocking success. Historically, however, Rainbow Trout perform poorly in FGR (Haddix and Budy 2005), and our reservoir-wide consumption estimates suggest that stocked Rainbow Trout could now be essentially feeding Burbot. If maintaining a put-and-take

Rainbow Trout fishery is the goal, trout stocked in late spring may have a greater chance of survival than those stocked in autumn due to seasonal diet preferences of Burbot, more opportunity for Rainbow Trout growth, and greater habitat segregation between Rainbow Trout and Burbot in summer. Conversely, populations of non-native Burbot could present a new sport fish (as they are classified by many agencies in their native range), and in FGR they offer the additional benefit of not require supplemental stocking.

While many anthropogenic influences play a role in the decline of Burbot in their native range, anthropogenic influences will also likely facilitate the range expansion of burbot to new ecosystems. Burbot are successful in FGR, but prey does not appear to be limiting in this system and other abiotic factors are suitable. Our population estimates of consumption suggest the potential for stronger trophic interactions with other top sport fishes, if the prey base decreases. If Burbot are introduced and/or expand into additional non-native waterbodies, they maybe be able to outcompete popular sport fishes if resources are limiting, or if sport fish populations are already limited by other factors (e.g., over-harvest, invasive species). As such, intentional introductions of Burbot to non-native ranges should be discouraged and prevented when possible; however, should they expand, our study provides a baseline understanding for management to adapt and preserve sport fisheries.

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<A> Tables and Figures

TABLE 1. Diet composition (percent prey weight and occurrence) by season and size class for Burbot sampled in Flaming Gorge Reservoir, WY-UT, in 2012 – 2013. Subcatergories within ‘fish’ are the percent occurrence by weight and count for fish prey items, and subcatergories within ‘salmonid *spp.*’ are the percent prey occurrences by weight and count for fish prey items that were salmonids. Percent by occurrence or by count values are in parentheses.

	Autumn	Winter	<400 mm	400 - 650 mm	>650 mm
Number of Burbot	188	197	52	278	55
Percent with prey	78	81	73	82	82
Total consumption (g)	1657	4199	150	3045	2363
Consumption per fish (g)	11.3	26.2	4.1	13.5	52.5
Mean length ± SE (mm)	494 ± 9	544 ± 9	351 ± 4	509 ± 4	720 ± 7
Prey by weight and occurrence (%)					
Crayfish	89.3 (77.6)	49.4 (85.0)	77.6 (78.4)	76.7 (83.6)	39.6 (71.1)
Fish	7.8 (32.7)	47.8 (48.9)	18.3 (27.0)	20.1 (35.6)	57.9 (77.8)
Burbot	22.7 (5.7)	8.6 (17.9)	15.1 (10.0)	16.7 (16.0)	4.8 (8.3)
Forage	68.6 (77.4)	11.9 (37.9)	20.4 (50.0)	26.8 (57.4)	9.0 (41.7)
Salmonid	0.0	71.7 (26.3)	0.0	32.5 (6.4)	86.0 (41.7)
Smallmouth Bass	5.6 (7.5)	7.0 (5.3)	51.5 (20.0)	21.5 (7.5)	0.0
Unidentified	3.1 (9.4)	0.8 (12.6)	13.0 (20.0)	2.5 (12.8)	0.1 (8.3)
Salmonid *spp.*					
Kokanee	0.0	0.0 (4.0)	0.0	0.0	2.8 (10.0)
Lake Trout	0.0	31.1 (28.0)	0.0	17.5 (16.7)	22.6 (25.0)
Rainbow Trout	0.0	60.5 (60.0)	0.0	59.7 (66.7)	67.8 (60.0)
Unidentified	0.0	8.4 (8.0)	0.0	22.8 (16.7)	6.8 (5.0)

TABLE 2. Lake Trout diets (percent prey occurrence) by size for Lake Trout sampled in Flaming Gorge Reservoir, WY-UT, in 2012 – 2013. Subcatergories within 'fish' are the percent occurrence by count for fish prey items, and subcatergories within 'salmonid *spp*.' are the percent prey occurrences by count for fish prey items that were salmonids.

	< 400 mm	400 - 650 mm	> 650 mm
Number of Lake Trout	9	17	11
Percent with prey	100	100	100
Total consumption (g)	6.6	40.4	2333
Consumption per fish (g)	0.7	2.4	212.0
Mean length ± SE (mm)	360 ± 11	535 ± 13	883 ± 42
Prey by weight and occurrence (%)			
Crayfish	0.0	11.0 (23.5)	0.0
Fish	23.5 (11.1)	84.0 (35.3)	100.0
Burbot	0.0	0.0	0.0
Forage	100.0	90.6 (83.3)	0.1 (3.4)
Salmonid	0.0	9.3 (8.3)	99.9 (96.6)
Smallmouth Bass	0.0	0.0	0.0
Unidentified	0.0	(0.1) 8.3	0.0
Salmonid *spp*.			
Kokanee	0.0	100.0	83.8 (85.7)
Lake Trout	0.0	0.0	10.5 (3.6)
Rainbow Trout	0.0	0.0	5.6 (10.7)
Unidentified	0.0	0.0	0.0
Zooplankton	76.5 (88.9)	5.0 (47.1)	0.0

TABLE 3. Age specific estimates for total, crayfish, fish, and other consumption by Burbot in Flaming Gorge Reservoir, WY-UT, scaled to estimated Burbot abundance in FGR. Values in parentheses represent the estimated range of possibilities.

Age	Total consumption (kg·10^4)	Crayfish consumption (kg·10^4)	Fish consumption (kg·10^3)	Other consumption (kg·10^3)
3	2.2 (1.3 - 9.4)	1.9 (1.1 - 7.7)	3.2 (1.8 - 13.2)	0.9 (0.5 - 3.8)
4	7.4 (4.2 - 30.6)	6.5 (3.7 - 26.8)	7.0 (4.0 - 28.9)	2.2 (1.3 - 9.2)
5	15.5 (8.9 - 64.7)	13.6 (7.8 - 56.6)	14.8 (8.5 - 61.6)	4.7 (2.7 - 19.4)
6	10.1 (5.8 - 42.0)	8.9 (5.1 - 36.7)	9.7 (5.5 - 40.3)	3.0 (1.7 - 12.6)
7	7.6 (4.4 - 31.6)	6.0 (3.4 - 24.8)	15.0 (8.6 - 62.3)	1.5 (0.9 - 6.3)
8	6.3 (3.6 - 26.2)	5.0 (2.8 - 20.5)	12.5 (7.1 - 51.8)	1.3 (0.7 - 5.3)
9	4.2 (2.4 - 17.2)	3.2 (1.9 - 13.5)	8.2 (4.7 - 34.0)	0.8 (0.5 - 3.4)
10+	4.7 (2.7 - 19.3)	3.6 (2.0 - 15.1)	9.2 (5.2 - 38.1)	0.9 (0.5 - 3.9)
TOTAL	58.1 (33.2 - 241.2)	48.6 (27.8 - 201.8)	79.5 (45.4 - 330.1)	15.4 (8.8 - 63.9)

<A> Figure Captions

FIGURE 1. Map of Flaming Gorge Reservoir, WY-UT. Shading represents each distinct region of the reservoir (Inflow, Open Hills, Canyon).

FIGURE 2. Diet proportions (% by wet weight; g) of total fish prey consumed by size class for **(a)** small Burbot (<400 mm; left), medium Burbot (400 – 650 mm; middle), and large Burbot (> 650 mm; right); and, **(b)** small Lake Trout (<400 mm; left), medium Lake Trout (400 – 650 mm; middle), and large Lake Trout (> 650 mm; right) captured in Flaming Gorge Reservoir, WY-UT (2012 – 2013). See Tables 1 and 2 for further breakdown of prey fishes, in particular, salmonids consumed by Burbot and Lake Trout > 650 mm.

FIGURE 3. Isotopic bi-plot of mean (± 2SE) carbon and nitrogen signatures of small, medium, and large Burbot, along with Lake Trout, Rainbow Trout, Smallmouth Bass, and Crayfish in Flaming Gorge Reservoir, WY-UT, 2012 – 2013.

FIGURE 4. Bioenergetic estimates of annual total consumption (kg) for the Burbot population in Flaming Gorge Reservoir, WY-UT, by age class (ages 3 – 10+) for: **(a)** crayfish and fish; **(b)** Burbot, forage fishes, salmonids, Smallmouth Bass; and, **(c)** salmonid prey including Kokanee Salmon, Lake Trout , Rainbow Trout. Note changes in the y-scale.

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