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

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38 <A>Abstract

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

60

61 <A>Introduction

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

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

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

84 2006). In accordance with the unnatural characteristic of reservoirs, stocked fishes often create a
85 mixed assemblage of native and non-native sport fishes, with almost entire non-native
86 assemblages relatively common (Martinez et al. 1994; Clarkson et al. 2005). Often times, these
87 mixed assemblages require annual stocking of predators, which can decouple the balance of
88 predator consumption demand and prey availability as seen in Lake Michigan (Johnson and
89 Martinez 2000).

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

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

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

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

126 In this study, we investigated the population status of Burbot in FGR, and assessed
127 potential direct and indirect impacts of Burbot on valued sport fish, with a primary focus on
128 trophy Lake Trout. We collected diet and stable isotope samples, and extended our findings
129 using a bioenergetics model to quantify predation potential and competition. Collectively, we

130 used these data to show how a newly established population of Burbot, across a range of
131 population densities, could affect highly managed sport fisheries, especially where annual
132 stocking promotes angler success. Our findings demonstrate that efficient predators such as
133 Burbot can consume many stocked sport fishes (e.g., Rainbow Trout) as well as important prey
134 resources (e.g., crayfish) for these sport fishes. If Burbot expansion continues to other
135 waterbodies, our study provides a baseline to better understand and manage the fishery.

136

137 <A>Methods

138 *Study site.*—

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

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

160

161 *Burbot catch and diet collection.*—

162 To assess population trend, diet composition, and total consumption by Burbot and Lake
163 Trout in FGR, we sampled fishes during two distinct seasons, autumn 2012 and winter 2013.
164 Autumn sampling occurred during 24 October – 15 November, 2012 and winter sampling
165 occurred during 15 January – 22 February, 2013. During autumn, we used multi-filament
166 trammel nets (33m long by 1.5m tall; internal mesh= 20mm, external mesh=100mm) set in the
167 littoral zone (5-25m) to collect fish. We set nets at established sampling sites in the Inflow and
168 Open Hills regions of the reservoir. Nets were set at dusk and fished overnight (approximately
169 1700-0900 hrs). Additionally, in conjunction with our sampling, we used data from long-term
170 autumn trammel net sampling (since 2006, Wyoming Department of Game and Fish and Utah
171 Division of Wildlife Resources (UDWR), unpublished data), to estimate population growth rate.
172 We estimated population growth rate (λ) based on the trend in corrected CPUE using a log-linear
173 regression-based trend model (Dennis and Taper 1994; Morris and Doak 2002). This analysis

174 provides support to better understand how population trend (e.g., population declining, stable, or
175 increasing) might affect reservoir wide consumption estimates.

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

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

187

188 *Diet analysis.*—

189 To characterize fish diet and selectivity, we identified prey items to the lowest taxon
190 possible and divided prey into representative categories (crayfish, fish, other). When possible,
191 we further divided these general categories (e.g., ‘fish’ by species, ‘other’ by group), measured
192 percent wet weight of each prey category for each individual fish, and then calculated diet
193 proportion and occurrence relative to the total sample size. We weighed prey fish individually.
194 For zooplankton and invertebrate prey, we weighed each taxonomic group en masse to the
195 nearest 0.001 g blot-dry wet weight. To estimate total consumption (g), we subtracted empty
196 stomach weight from full stomach weight, or summed the weight of all prey items (e.g., diets

197 obtained via gastric lavage). We analyzed Burbot diets for temporal (autumn vs. winter) and size
198 class (<400 mm = small, 400-650 mm = medium, and >650 mm = large) variability. Due to
199 lower sample size, we analyzed Lake Trout diets by size class, but pooled across season and site.
200 To determine potential interspecific competition between Burbot and Lake Trout, we calculated
201 diet overlap using Schoener's index, α (Schoener 1970):

$$202 \quad \alpha = 1 - 0.5 \cdot (\sum_{i=1}^n |p_{xi} - p_{yi}|),$$

203 where i is a given prey item, p is the proportion of i , and x and y are Burbot and Lake Trout. The
204 single value α is diet overlap from 0 (no overlap) to 1 (complete overlap), and values greater than
205 0.6 are indicative of significant diet overlap (Schoener 1970).

206

207 *Stable isotopes.*—

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

$$217 \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \cdot 1000 ,$$

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

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

$$222 \quad TP_i = \left(\frac{\delta^{15}N_i - \delta^{15}N_{baseline}}{3.4} \right) + 1,$$

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

228 To evaluate characteristics trophic overlap of Burbot with other sport fishes, we used
229 SIBER (Stable Isotope Bayesian Ellipses) in R, which uses Bayesian inference techniques to
230 describe niche and community metrics (Jackson et al. 2011). The SIBER model uses bivariate
231 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data to represent isotopic trophic niche space for a species or group. The SIBER
232 model produces ellipses around the centroid that include ± 1 SD. We calculated the percent
233 species overlap at the intersection of ellipse areas. Kokanee Salmon were not included in this
234 analysis owing to low sample size; however, our initial plots showed no potential overlap.

235

236 *Bioenergetics.*—

237 We modified equations from Bioenergetics 3.0 (Hanson et al. 1997) to run in R version
238 3.2.1 (R Development Core Team, 2015) to estimate annual Burbot consumption (kg; Kitchell et
239 al. 1977). We used physiological parameters from Rudstam et al. (1995). To estimate reservoir-
240 wide annual consumption by Burbot, we first estimated size-specific annual consumption based

241 on individual Burbot, and then applied these estimates to an age structure and abundance index
242 of Burbot within FGR. First, annual growth (mm) was approximated using the difference
243 between modes from a length-frequency histogram of our 2012 – 2013 catch, and we determined
244 mean length at age for each year class from 1000 randomly drawn lengths from normally
245 distributed Burbot lengths for estimated year classes. We corroborated these growth estimates
246 using otoliths and mark-recapture information from Burbot tagged during 2011 – 2016 (UDWR,
247 unpublished data). Mark-recapture data is derived from annual UDWR Burbot fishing derbies, in
248 which ‘prize fish’ are tagged and released for a given year’s tournament, but often caught during
249 subsequent years (1 – 4 years growth; n = 37, length at first capture = 279 – 731 mm TL). These
250 data provide accurate estimates of yearly growth, which we used to corroborate length-frequency
251 modes. We applied age-3 to our smallest size class sampled, and our largest fish were grouped to
252 a size class of age-10+. Otoliths confirmed that our sampling methods captured burbot age-3 and
253 older (Luecke and Mears 2011), and our length-frequencies modes appropriately fit the FGR
254 Burbot population. We then fit a von Bertalanffy growth model (Ricker 1975) for final length-at-
255 age predictions:

$$256 \quad \text{burbot length} = 1065.58 \cdot (1 - e^{-(0.13 \cdot (\text{burbot age} - 0.16))}),$$

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

$$261 \quad \text{burbot weight} = e^{-12.32 + 3.02 \cdot \log_e(\text{burbot length})},$$

262 For bioenergetic analyses, we combined Burbot diet proportions (% wet weight, g), as
263 described above, by length (e.g., < 400, 400 – 650, > 650 mm) and season (e.g., fall, winter). We

264 used temperature profiles (early May to early December; 2009 – 2015; UDWR, unpublished
265 data) in bi-weekly periods averaged across years to obtain a ‘typical’ thermal experience for
266 Burbot and extrapolated water temperatures for dates in between. Between December 15 and
267 March 15, we assumed the reservoir was ice covered or completely mixed at or below 4°C.
268 Throughout the remainder of the year, we assumed Burbot behaviorally thermoregulated to live at
269 the optimal temperature for gadoids (13.7°C; Rudstam et al. 1995, but see Harrison et al. 2016).
270 When optimal temperature was not available in the water column, we assumed Burbot would
271 occupy the temperature nearest to 13.7°C (e.g., 4°C from December 15 – March 15).

272 As a coarse index of relative Burbot abundance and density in FGR, we applied the
273 Schumacher and Eschmeyer method (Krebs 1999) using mark-recapture of tagged Burbot
274 (UDWR, unpublished data). While we acknowledge we violated some assumptions of this
275 method, confounding factors (e.g., catch and kill regulation) limited our overall ability to use a
276 more robust method. Nonetheless, our index of abundance (mean = 140,000 individuals; range =
277 80,000 – 510,000 individuals; 95% CI) provides density estimates similar to other studies where
278 Burbot are successful in their native range (e.g., Parker et al. 1989; Rudstam et al. 1995).
279 Further, this estimate provides us a relative measure of the potential impact of the total
280 population (e.g., a low and high estimate). To estimate annual consumption across the reservoir,
281 we multiplied bioenergetic estimates of consumption for the mean length fish for each age class
282 (3 – 10+ years old) by the proportion of sampled Burbot in each age class and by the range of
283 total population estimates. Due to smaller sample size and growth approaching the asymptote of
284 our von Bertalanffy growth model, we pooled fish age 10 and greater to a single age category
285 (e.g., Madenjian et al. 2011)

286

287 <A>Results

288 Burbot Catch and Diets

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

294 We examined stomach contents from 385 Burbot (518 mm \pm 5.8 [mean TL \pm 1 SE];
295 range = 307 – 850 mm) collected during autumn 2012 (n = 188) and winter 2013 (n = 197). Of
296 these, 307 stomachs contained diet items, while 78 were empty; we excluded empty stomachs
297 from further diet analyses. Of the Burbot stomachs that contained prey items, Northern Crayfish
298 (81.4 % by occurrence) were most often consumed, followed by fish (40.1 % by occurrence;
299 Table 1). However, we noted variation in diet composition and consumption across time and size
300 classes.

301 We analyzed diets from 78 % of Burbot captured in autumn (n = 147) and 81% of Burbot
302 captured in winter (n = 160). Total mean consumption by Burbot was significantly greater ($t_{\text{DF} =$
303 $189} = 3.70$, $P < 0.01$) in winter than during autumn (Table 1; 26.2 ± 3.9 vs. 11.3 ± 1.2 g [mean \pm
304 1 SE]); however, mean length of Burbot captured in winter was also greater than in autumn.
305 During autumn, Burbot most often consumed crayfish (89.3% by weight) and some fish (7.8%
306 by weight). In winter, Burbot consumption of crayfish (49.4% by weight) was considerably less
307 than autumn, and similar to consumption of fishes during winter (47.8% by weight).
308 Consumption of fish was more than six-fold greater during winter relative to autumn.

309 Prey fish composition in Burbot diets, and total consumption of fishes, also varied by
310 season (Table 1). During autumn, of fish consumed, Burbot primarily consumed forage fishes
311 (e.g., sucker and chub spp.; 68.6% by weight). We observed no consumption of salmonids, and
312 the only sport fish we identified in autumn diets was Smallmouth Bass (5.6% by weight).
313 However, during winter salmonids composed the greatest proportion of fish in Burbot diets
314 (71.7% by weight). Burbot still consumed forage fishes, but in lesser proportion than autumn
315 (11.9% by weight). Of the salmonids consumed during the winter, Rainbow Trout (60.5% by
316 weight) and Lake Trout (31.1% by weight) made up the majority of salmonids consumed.
317 Overall, cannibalism was approximately three times more common in winter than autumn (17.9
318 % vs 5.7 % occurrence) but made up a greater proportion of the total diet in autumn (22.7% vs.
319 8.6% by weight).

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

332 (21.5% by weight) with similar frequency. In contrast, large Burbot predominately consumed
333 salmonids (86% by weight), while forage fishes comprised the only other significant fish prey
334 (9.0% by weight). Of the salmonids consumed, most were Rainbow Trout (67.8% by weight)
335 and Lake Trout (22.6% by weight), and this pattern was similar for salmonids consumed by
336 medium Burbot (59.7% and 17.5% by weight, respectively).

337

338 Lake Trout Catch and Diets

339 We analyzed a total of 37 Lake Trout diets from trammel net and hook-and-line sampling
340 in autumn and winter 2012-2013 (Table 2). Small Lake Trout (<400 mm; n = 9) consumed
341 mostly zooplankton (76.5% by weight) and few fish (23.5% by weight), medium-sized Lake
342 Trout (400-650 mm; n = 17) consumed mostly fish (84.0% by weight) and few crayfish (11.0%
343 by weight; Figure 2b). When consuming fishes, small and medium-sized Lake Trout almost
344 entirely consumed forage fishes (95.2% by weight). Large, trophy Lake Trout (>650 mm, mean
345 TL = 883.6 ± 42.4 mm; n = 11) consumed fish exclusively (100% by weight), and mean total
346 consumption by large Lake Trout was much greater than large Burbot (212.1 ± 63.24 vs. $52.5 \pm$
347 10.0 g) These large Lake Trout consumed almost entirely other salmonids (>99.9% by weight),
348 with most of these salmonids being Kokanee Salmon (83.8% by count). We did not observe
349 consumption of Burbot by Lake Trout.

350

351

352

353 Potential Competition and Bioenergetics

354 Based Schoener's index, we observed no potential for interspecific competition, and very
355 little overall diet overlap, between Burbot (all sizes pooled) and Lake Trout (all sizes pooled; $\alpha =$
356 0.13). We also observed very little overlap when comparing small, medium, and large Burbot
357 separately to all Lake Trout ($\alpha = 0.01, 0.06, \text{ and } 0.19$, respectively). This notion matches our
358 diet analyses; large Lake Trout consumed mostly Kokanee Salmon, while Kokanee Salmon
359 accounted for less than 3% of salmonids consumed by large Burbot (Tables 1, 2). $\delta^{15}\text{N}$
360 signatures and thus, trophic positions, of small (TP = 2.16 ± 0.07 [mean \pm 1 SE]), medium (TP =
361 2.63 ± 0.26 [mean \pm 1 SE]), and large Burbot (TP = 2.99 ± 0.07 [mean \pm 1 SE]), were
362 significantly different ($F_{(2,43)} = 15.7, P < 0.005$), and $\delta^{13}\text{C}$ signatures indicated Burbot may
363 compete more with littoral Rainbow Trout and Smallmouth Bass than pelagic Lake Trout (Figure
364 3). Large Lake Trout trophic position (TP = 3.24 ± 0.06 [mean \pm 1 SE]) was significantly
365 greater than that of large Burbot ($t_{(189)} = 2.63, P = 0.02$). Rainbow Trout trophic position (TP =
366 2.22 ± 0.38 [mean \pm 1 SE]) was similar to small Burbot ($t_{19} = 0.43, p = 0.67$), and Smallmouth
367 Bass trophic position (TP = 2.49 ± 0.07 [mean \pm 1 SE]) was similar to medium Burbot ($t_{12} =$
368 $1.36, P = 0.20$). Additionally, our analyses of trophic niche space showed no overlap between
369 Burbot (of any size group) and Lake Trout. However, we did note diet overlap between Burbot
370 and Rainbow Trout, and Burbot and Smallmouth Bass. Specifically, small Burbot and medium
371 Burbot niche space overlapped with 21.8% and 17.9% of Rainbow Trout niche space, and
372 medium Burbot also overlapped with 44% of Smallmouth Bass niche space (see Appendix 1).

373 Annual consumption by Burbot, on an individual basis, increased with age (1622 – 8318
374 $\text{g}\cdot\text{yr}^{-1}$, age-3 – age-10+), and age specific bioenergetic efficiency (proportion of maximum
375 consumption, *BioEff*; Budy et al. 2013) decreased with age, but was relatively high overall

376 ($BioEff = 0.57 - 0.69$; age-10+ and age-3; see Appendix 2). Overall, at the population level, we
377 estimate that Burbot consumed between $3.3 \cdot 10^5 - 2.4 \cdot 10^6$ kg of prey annually (mean = $5.8 \cdot$
378 10^5 kg). Crayfish accounted for 84% of annual Burbot consumption, while fish and other prey
379 items accounted for 14% and 2% of annual Burbot consumption (Table 3; Figure 4a). When
380 consuming fishes, 62% of annual Burbot consumption was salmonids (66% Rainbow Trout, 22%
381 Lake Trout, 10% unidentified, and 2% Kokanee Salmon, respectively; Figure 4c) while 17% was
382 forage fishes, 10% other Burbot, 10% Smallmouth Bass, and 1% unidentified. Age-5 Burbot
383 (451 – 524 mm; mean = 490 mm) made up the greatest proportion of the overall population
384 (30%), and also consumed the most prey biomass annually ($1.5 \cdot 10^5$ kg). Age-3 Burbot (307 –
385 367 mm; mean = 324 mm; 10% of the population) consumed the least prey biomass annually
386 ($2.27 \cdot 10^4$ kg). Age-5 and age-7 (589 – 646 mm; mean = 619 mm) Burbot consumed the most
387 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-
388 7 fish prey was salmonid while only $4.86 \cdot 10^3$ kg was salmonid for age-5 Burbot (Figure 4b).

389

390 <A>Discussion

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

399 as well as large quantities of important sport fish prey resources (e.g., crayfish), which could
400 disrupt predator-prey dynamics and the food web within FGR.

401 Since the expansion of Burbot into FGR, there has been concern and uncertainty about
402 the potential trophic impacts of this novel predator with regard to popular sport fishes. In FGR,
403 the Lake Trout population is popular, long-established and stable, and no longer requires
404 stocking to supplement the fishery. In contrast, the Lake Trout population in Lake Michigan,
405 where Burbot and Lake Trout are both native, has declined as a result of the invasion of other
406 species that lead to the decimation of Lake Trout prey (Rogers et al. 2014; Tsehaye et al. 2014).
407 As such, while these species previously co-existed here in their native range (see also Cott et al.
408 2011; Guzzo et al. 2016), today Burbot consumption of Lake Trout likely limits rehabilitation
409 efforts in Lake Michigan via direct consumption of an already diminished Lake Trout population
410 (Jacobs et al. 2010). Our results indicate that Burbot and Lake Trout can live in sympatry, in
411 their non-native ranges, especially when prey is not limiting and Lake Trout populations are
412 stable and performing well (e.g., biotic resistance; Fausch 2008). Accordingly, this study and
413 others (e.g., Yule and Luecke 1993) demonstrate Lake Trout feed predominately on Kokanee in
414 FGR, and as such, maintaining a healthy Kokanee population is important for Lake Trout
415 success. On the other hand, Burbot consume other sport fishes, such as Rainbow Trout, in large
416 quantities.

417 While our study shows that Burbot in FGR primarily consume crayfish, there is potential
418 for direct and indirect competition with other sport fish. From 2006 – 2012, an average of
419 535,060 (377,906 – 821,121) Rainbow Trout were stocked annually in FGR (UDWR,
420 unpublished data). Assuming these trout are stocked at a catchable size of 200 mm, and weigh
421 approximately 120 g each, an average of 64000 kg of Rainbow Trout are stocked annually. Our

422 bioenergetic analyses indicate the population of Burbot in FGR could consume 29% of these
423 Rainbow Trout at a low Burbot abundance estimate and more than double the biomass of the
424 total Rainbow Trout (> 1 million individuals) stocked annually at the high end of this estimate.
425 Furthermore, competition for food resources between Smallmouth Bass and Burbot could also be
426 substantial, as crayfish are often the primary prey of Smallmouth Bass (Garvey et.al. 2003), and
427 Burbot in FGR could consume more than 117 kg · ha⁻¹ of crayfish annually.

428 In their native range, Burbot show the potential to feed opportunistically and outcompete
429 other fishes for desired prey (Knudsen et al. 2010); thus, in non-native waters, the potential for
430 burbot to fill open niche space could contribute to their expansion success (e.g., Vatland and
431 Budy 2007). In FGR, crayfish are relatively abundant and, for benthic predators such as Burbot,
432 relatively easy to capture. On the other hand, because Burbot consume primarily crayfish in
433 FGR, there could be unknown consequences should the crayfish population decline dramatically
434 (e.g., Hein et al. 2007). Conversely, Paragamian (2010) suggests a strong link between Burbot
435 and crayfish in that crayfish abundance increased in Kootenai River following a decline in
436 Burbot. Our bioenergetic analyses suggests high levels of reservoir-wide crayfish consumption,
437 but we have inadequate information on the availability of crayfish across and within years to
438 truly understand how crayfish abundance might control Burbot. However, if crayfish became
439 limited, it is plausible, based on our dietary analyses, that burbot in FGR could shift to other prey
440 (e.g., increased piscivory on sport fish). Cott et al. (2011) demonstrated Burbot can play a role in
441 structuring fish communities with other top predators, and in the Great Lakes, Burbot diets
442 shifted correspondingly as proliferation of new invasive species created abundant new prey (e.g.,
443 Round Gobies; Jacobs et al. 2010; Hares et al. 2015). Previous work in FGR demonstrated an
444 increase in juvenile forage fishes following a high water year resulting in increased forage fish

445 recruitment. The following autumn, greater consumption of forage fish was observed, suggesting
446 Burbot opportunistically consumed abundant prey fish (Luecke and Mears 2011). Accordingly,
447 variability in Burbot diets may be due to variability in prey abundance and availability
448 (Pääkkönen 2000); however, in FGR we would need a better understanding of overall prey
449 availability to make better determinations of prey selectivity versus availability.

450 Across seasons, prey selection could be driven by Burbot life history and/or metabolic
451 demands. Previous work on FGR found that consumption by Burbot increased from summer to
452 autumn (Luecke and Mears 2011); however, in the past, too few winter samples were available
453 to make strong seasonal comparisons. Summer temperatures in the top 10 m of the water
454 column may be too warm for daily vertical migrations to forage, as has been documented in
455 cooler waterbodies of Canada where Burbot are native (Harrison et al. 2013). The increase in
456 consumption from summer to autumn is likely associated with cooling of water temperatures
457 towards the thermal optimum of Burbot, an obligate cold water fish (McPhail and Paragamian
458 2000). We hypothesize that Burbot consumption further increases in winter, as prey metabolism
459 slows and as they are recovering from winter spawning activities that are energetically costly
460 (Saunders et al. 2014). We also observed increased Burbot cannibalism during winter, which
461 may reflect opportunistic feeding and/or greater intraspecific competition as a result of spawning
462 congregation (Hofmann and Fischer 2001; Cott et al. 2013; Gallagher and Dick 2015)

463 Our observed differences in Burbot diets and consumption across sizes are likely driven
464 by ontogenetic shifts in behavior. During 2012-2013, small and medium Burbot fed primarily on
465 crayfish prey, while large Burbot were primarily piscivorous. While it is possible small and
466 medium size classes of Burbot may be gape limited; we also observed fish in the diets of Burbot
467 as small as 301 mm, and 11% of Burbot less than 400 mm consumed fish. However, the

468 majority of fish prey consumed by these size classes were bottom and littorally oriented fishes.
469 Small and medium Burbot may avoid feeding in profundal zones to avoid predation themselves
470 and cannibalism, while large Burbot can likely forage more freely and successfully in the littoral
471 with predation fear (Harrison et al. 2013). Overall, the physiological ability of Burbot, across
472 size classes, to consume prey (e.g., gape limitation) corroborates the concept that they are highly
473 effective predators, as has been demonstrated herein and elsewhere (e.g., Kahilainen and
474 Lehtonen 2003). This effective predation may necessarily influence management strategies (e.g.,
475 size of fish stocked). As an illustration, in FGR, we observed large Burbot consuming fish
476 greater than 50% of their own total body length. In winter 2013, a 780 mm Burbot consumed an
477 approximately 420 mm Rainbow Trout, more than double average length at stocking, suggesting
478 rainbow trout that overwinter still remain susceptible to predation.

479

480 *Management Implications.*—

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

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

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

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536 <A> Tables and Figures

537 TABLE 1. Diet composition (percent prey weight and occurrence) by season and size class for
 538 Burbot sampled in Flaming Gorge Reservoir, WY-UT, in 2012 – 2013. Subcategories within
 539 ‘fish’ are the percent occurrence by weight and count for fish prey items, and subcategories
 540 within ‘salmonid *spp.*’ are the percent prey occurrences by weight and count for fish prey items
 541 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
<u>Prey by weight and occurrence (%)</u>					
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 <i>spp.</i>					
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)

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550 TABLE 2. Lake Trout diets (percent prey occurrence) by size for Lake Trout sampled in Flaming
 551 Gorge Reservoir, WY-UT, in 2012 – 2013. Subcategories within ‘fish’ are the percent
 552 occurrence by count for fish prey items, and subcategories within ‘salmonid *spp.*’ are the
 553 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
<u>Prey by weight and occurrence (%)</u>			
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 <i>spp.</i>			
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

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561 TABLE 3. Age specific estimates for total, crayfish, fish, and other consumption by Burbot in
 562 Flaming Gorge Reservoir, WY-UT, scaled to estimated Burbot abundance in FGR. Values in
 563 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)

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565 <A> Figure Captions

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

568

569 FIGURE 2. Diet proportions (% by wet weight; g) of total fish prey consumed by size class for **(a)**
570 small Burbot (<400 mm; left), medium Burbot (400 – 650 mm; middle), and large Burbot (> 650
571 mm; right); and, **(b)** small Lake Trout (<400 mm; left), medium Lake Trout (400 – 650 mm;
572 middle), and large Lake Trout (> 650 mm; right) captured in Flaming Gorge Reservoir, WY-UT
573 (2012 – 2013). See Tables 1 and 2 for further breakdown of prey fishes, in particular, salmonids
574 consumed by Burbot and Lake Trout > 650 mm.

575

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

579

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

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