North American Journal of Fisheries Management 40:1161–1173, 2020

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10480

ARTICLE

Movement Dynamics of Nonnative Burbot in the Upper Green River System and Implications for Management

Tucker A. Brauer*[1]
Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Moscow, Idaho 83844, USA

Michael C. Quist
U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Moscow, Idaho 83844, USA

Darren T. Rhea
Wyoming Game and Fish Department, 432 East Mill Street, Pinedale, Wyoming 82941, USA

Troy W. Laughlin
Wyoming Game and Fish Department, 351 Astle Avenue, Green River, Wyoming 82935, USA

Erik Waring
Wyoming Game and Fish Department, 432 East Mill Street, Pinedale, Wyoming 82941, USA

Abstract
Burbot *Lota lota* were illegally introduced to the Green River, Wyoming, in the mid-1990s and pose a threat to recreational fisheries and native fish conservation. Although much is known about Burbot population dynamics, little is known about their movement patterns. Our objectives were to describe the movement dynamics of Burbot in the upper Green River system to provide information on the ecology of Burbot and insight on possible management actions. In total, 875 Burbot were tagged with PIT tags in the upper Green River and Fontenelle Reservoir; their movements were tracked from August 2016 to March 2018. Additionally, 22 Burbot were tagged with radio transmitters in Fontenelle Reservoir in November 2017, and 13 Burbot were tagged with radio transmitters in the upper Green River in November 2018. Of these fish, 11 Burbot tagged in Fontenelle Reservoir and all river-tagged Burbot were tracked as they migrated into the Green River and associated tributaries during the spawning season. Upstream and downstream movements of Burbot tagged with PIT tags in Fontenelle Reservoir and the upper Green River peaked during December–January and were synchronized with river temperatures reaching 0°C. Of the total number of PIT-tagged Burbot, 10–15% of those tagged in Fontenelle Reservoir were detected in the Green River during the spawning season and 15% of those tagged in the Green River were detected moving downstream toward Fontenelle Reservoir during the spawning period. Movements of radiotelemetered Burbot were synchronized with river ice-up in mid-December. Maximum upstream distance traveled by adfluvial Burbot was 5.8 km. Fluvial Burbot primarily migrated downstream during the spawning period, and maximum downstream distance traveled was 17.7 km. Detection data suggest that both fluvial and adfluvial Burbot occupy the same reaches

*Corresponding author: tucker.brauer@state.nm.us
[1]Present address: New Mexico Department of Game and Fish, 1 Wildlife Way, Santa Fe, New Mexico 87505, USA.
Received January 21, 2020; accepted June 8, 2020

during the spawning period and areas near Fontenelle Reservoir are important for spawning. Results of this study will assist with the management of Burbot in this system by shedding light on Burbot movement patterns and identifying areas of high Burbot use for targeted suppression efforts. Results also contribute to our understanding of the variability in Burbot ecology.

Freshwater fishes exhibit a diversity of movement behaviors and life history strategies (Mann et al. 1984). These life history strategies are often of interest to fishery managers due to the influences that individual movement behaviors may have on population status (Pine et al. 2012). Freshwater fish generally employ one of four life history strategies, including resident (i.e., river dwelling and spawning), fluvial (i.e., river dwelling, tributary spawning), adfluvial (i.e., lake dwelling, river or stream spawning), and anadromous (i.e., ocean dwelling, river spawning) variants. Each life history variant group in a population can be affected by different factors, and managers must understand the population's structure to ensure effective management (Jonsson 1985; Trotter 1989; McPhail and Baxter 1996; Peterson et al. 2007). For example, adfluvial Bull Trout *Salvelinus confluentus* in Lower Kananaskis Lake, Alberta, were subject to high exploitation rates during their spawning season as they became more vulnerable to angling in the shallow tributaries compared to the deepwater habitat they used during the nonspawning season. By closing the fishery in tributary streams, the population experienced a 28-fold increase in abundance over a 10-year period (Johnston et al. 2007). Similarly, a review by Cunjak (1995) suggested that increases in salmonid production brought on by summer habitat improvement projects were frequently nullified by a lack of overwinter habitat and subsequent movements of fish out of rehabilitated reaches. Such examples highlight the importance of understanding life history and movement dynamics when managing fish populations.

In addition to managing socially important fishes, assessments of population structure and movement dynamics are also crucial when designing removal programs that target undesirable species, especially when that species is known to exhibit multiple life history strategies. Understanding movement dynamics and population structure of undesirable species can often make removal efforts more effective. For example, Lake Trout *S. namaycush* inhabit deep lakes throughout a majority of the year and are less susceptible to most sampling gears; however, they often congregate in shallow waters to spawn and are vulnerable to removal efforts at that time (Gunn 1995). Numerous nonnative Lake Trout populations throughout the western United States have been targeted for removal by focusing suppression efforts on spawning aggregations (Syslo et al. 2011). Similar methods have been used to suppress Common Carp *Cyprinus carpio* in the Midwestern United States. Bajer et al. (2011) achieved 52–94% removal from four Midwestern reservoirs by targeting winter-time aggregations of Common Carp using commercial seines. Effective suppression programs such as these provide a model for fishery managers that are addressing the effects of nonnative species in their own jurisdictions. Nonnative Burbot *Lota lota* inhabiting the Green River basin (GRB), Wyoming, serve as one such example where an understanding of movement dynamics and population structure is critical for developing effective suppression programs.

Burbot are native to northern Wyoming in the Wind–Big Horn and Tongue River basins (Baxter and Stone 1995). Like many native populations of Burbot in the United States, Burbot populations in Wyoming have declined. They have been extirpated from the Tongue River system and occur at low densities in the Wind–Big Horn River drainage, which has prompted their designation as a "species of greatest conservation need" in Wyoming (Krueger and Hubert 1997; Hubert et al. 2008; Underwood et al. 2016; WGFD 2017). In these systems, management is focused on conservation and protection of native Burbot populations. Burbot are also present in the GRB due to unauthorized introductions in the 1990s, where they elicit a very different management response given their invasive nature (Gardunio et al. 2011). The Green River is home to a variety of endemic species and popular sport fish species, many of which Burbot are known to prey upon (Gardunio et al. 2011; McBaine et al 2018). A recent study by Klobucar et al. (2016) found evidence that Burbot diets directly overlapped with those of Smallmouth Bass *Micropterus dolomieu* and that Burbot have the capacity to consume over double the biomass of Rainbow Trout *Oncorhynchus mykiss* stocked annually in Flaming Gorge Reservoir, Utah–Wyoming (>1 million fish). Given the potential of Burbot to negatively affect socially and ecologically important fishes in the Green River system through predation and competition, the Wyoming Game and Fish Department (WGFD) has expressed interest in a suppression program to target Burbot (Klein et al. 2015a, 2015b, 2016; Brauer et al. 2019). However, before a suppression effort can be implemented, an in-depth understanding of the movement dynamics and population structure of Burbot must be attained to effectively allocate suppression efforts.

Burbot is a holarctically distributed top predator that occurs throughout a diversity of lotic and lentic habitats

(McPhail and Paragamian 2000). Similar to gadiforms in marine environments (e.g., Atlantic Cod *Gadus morhua*), Burbot have exhibited both resident and migratory behavior (Cote et al. 2004). In some lotic systems, fluvial Burbot migrate long distances to spawning sites, sometimes traveling over 100 km (Evenson 1993). Some lacustrine populations of Burbot have demonstrated an adfluvial life history wherein they occupy a lake and use tributary streams for spawning (Paragamian 2000; Schram 2000). Burbot spawn in aggregate during the winter (McPhail and Paragamian 2000), and these aggregations represent a potential target for suppression efforts, as targeting these sites will likely increase the efficiency of removal efforts. However, the locations of spawning areas in the GRB are unknown. Since 2001, Burbot have been consistently sampled in both the Green River and its associated reservoirs (i.e., Fontenelle and Flaming Gorge reservoirs; Gardunio et al. 2011; Klein et al. 2016; Brauer et al. 2019). Anecdotal evidence also suggests that proportions of Burbot in the upper Green River system exhibit both adfluvial and resident movement behaviors (Klein et al. 2015b). Movements of Burbot between reservoir and river environments may influence the effectiveness of removal efforts by informing previously developed population models (Klein et al. 2016; Brauer et al. 2019). If Burbot in the upper Green River system exhibit migratory behavior, understanding movement patterns and locating high-use areas (i.e., spawning locations) will help with management of the system. Movement may also influence Burbot population dynamics in the GRB due to the addition and(or) subtraction of individuals from reservoir and river environments. The goal of this study was to provide information to aid Burbot suppression efforts in the upper Green River system. Our objectives were to (1) describe timing and patterns of Burbot movement using both PIT tags and radiotelemetry and (2) identify areas of high use by Burbot that may serve as targets for suppression. Satisfying both objectives will add to knowledge of Burbot ecology outside the species' native range.

METHODS

Study area.— The Green River is the largest tributary to the Colorado River, draining portions of Colorado, Utah, and Wyoming. The upper Green River originates in the Wind River Range of western Wyoming and flows approximately 235 km before entering Fontenelle Reservoir (Figure 1). Fontenelle Reservoir is an artificial impoundment primarily used for flood control with a secondary use of hydroelectric power generation. At capacity, the reservoir has a surface area of approximately 3,200 ha and a maximum depth of about 30 m. Upstream of Fontenelle Reservoir, the Green River is characterized by high-gradient runs interspersed with pool–riffle habitat and substrate dominated by alluvial deposits (i.e., cobble, gravel, sand, and silt; Kurtz 1980). Most of the GRB is typical of a high-desert climate, with monthly average temperatures of −9°C (January) and 17°C (July) and low annual precipitation (25.4 cm; WGFD 2017). During the winter season, the majority of the upper Green River and Fontenelle Reservoir is covered with ice. Ice-up generally occurs in late November to early December, and ice-out typically occurs in March along with low-elevation runoff.

Data collection.— A dual application of PIT and radiotelemetry technology was used to describe Burbot movements in this system. Passive integrated transponder tags were intended to describe coarse-scale movement patterns of Burbot tagged in the Green River and Fontenelle Reservoir. Radiotelemetry was used to describe fine-scale movement patterns of fluvial Burbot in the Green River and adfluvial Burbot in Fontenelle Reservoir. We were primarily interested in identifying spawning areas, the timing of migration, and the extent of migrations undertaken by Burbot.

In July 2016, two identical flat-panel, half-duplex PIT antennae were installed in the Green River 7 km upstream of Fontenelle Reservoir (Figure 1) and were active from July to March in 2016–2018 except during periods of high runoff. The site was chosen due to its proximity to Fontenelle Reservoir, comparatively narrow channel, accessibility, and landowner cooperation. Each antenna covered one-half the river channel (~50 m each). Antennae were configured in a pass-over design that minimized potential damage from high velocities. Antenna efficiency was measured using a large-scale detection test modified from Compton et al. (2008). Briefly, a PIT tag was passed over the antenna at 1-m intervals at substrate, mid-column, and surface depths. The tag was held parallel and perpendicular to the antenna at each location. Combined detection efficiency for the array was 86% under base flow conditions (mean discharge = 9.9 m^3/s; maximum depth at testing = 0.5 m) and effective read range was approximately 30 cm. The system did not differentiate between upstream and downstream movements. Movement direction was inferred by release location or last detection of tagged fish. Antennae recorded movements of Burbot for the project duration except for periods of high flow (spring–summer season), when they were removed to avoid damage to PIT electronics.

Burbot were PIT-tagged in the upper Green River in the summer of 2016 and 2017 and in Fontenelle Reservoir during the fall of 2016 and 2017. Fish in the upper Green River were collected using drift-boat-mounted electrofishing gear in the section of river beginning at the PIT antenna array to a point 50 km upstream of the array. Power output was standardized to 2,750–3,250 W (Miranda 2009), and sampling took place after sunset to maximize catch rates (Witt and Campbell 1959; Paragamian

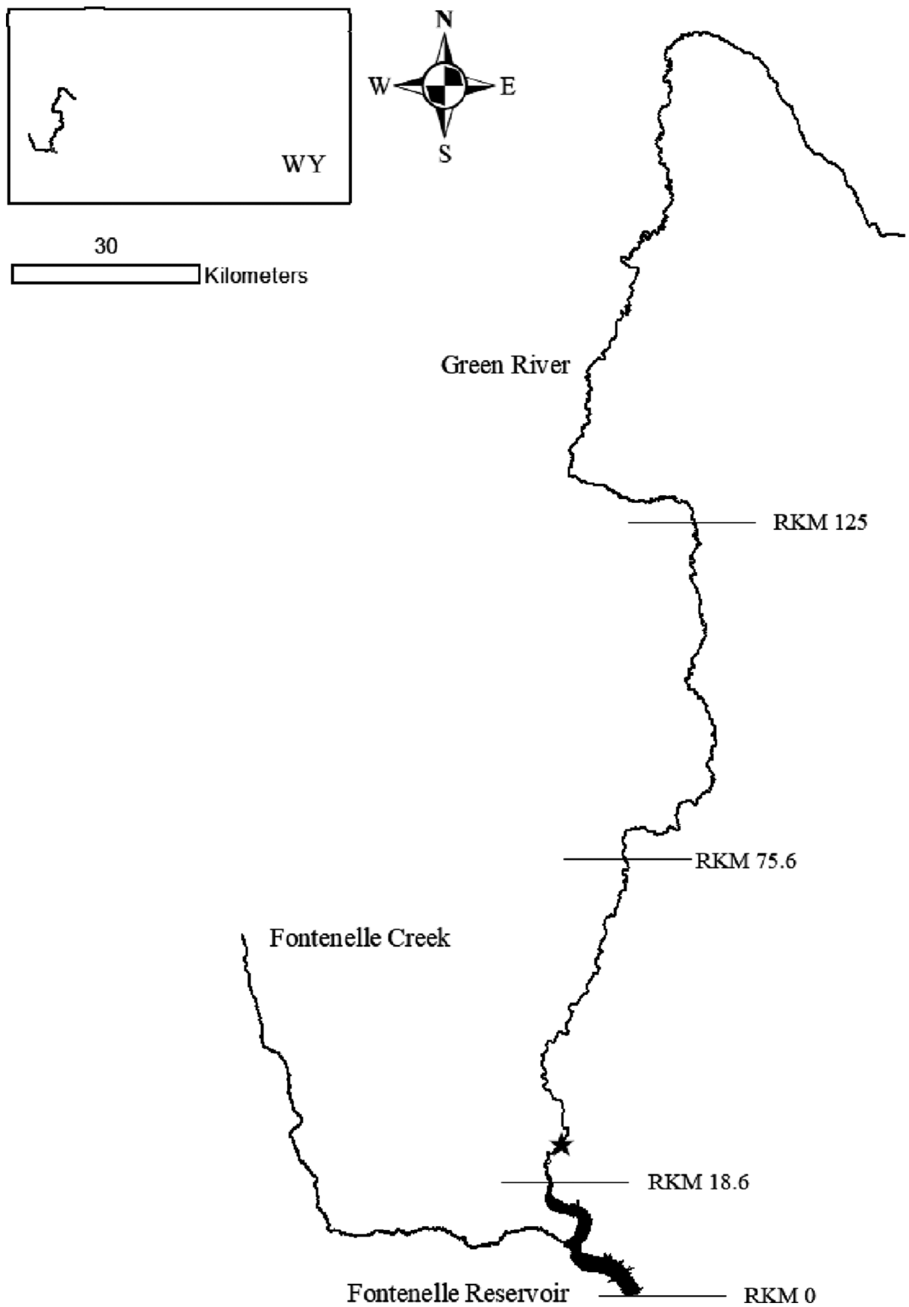

FIGURE 1. Map of the upper Green River and Fontenelle Reservoir, Wyoming, study area, where Burbot were sampled during summer and autumn (2016–2018). Horizontal lines represent river kilometer (RKM) boundaries of telemetry tracking via foot-based methods (RKM 18.6–75.6) and aerial methods (RKM 0–125); RKM 0 represents Fontenelle Dam, and RKM 18.6 represents the mouth of the Green River during the study period. The location of a PIT antenna array is indicated by a star.

1989; Klein et al. 2015a). Fish in Fontenelle Reservoir were collected using trammel nets. Trammel nets were 48.8 m long and 1.8 m tall and consisted of 25.4-cm bar outer mesh and 2.5-cm bar inner mesh. Nets were set perpendicular to shore at varying depths (<20 m) and anchored at both ends. Net locations were placed in standardized locations used by WGFD during annual Burbot surveys or near those locations when additional netting effort was required.

All captured Burbot were enumerated, measured for TL (mm) and weight (g), and implanted with a 23-mm, half-duplex PIT tag (Oregon RFID, Portland). Tags were injected into the peritoneal cavity just off the midline and posterior to the pectoral fin using a syringe applicator due to the high retention rate (>95%; Ashton et al. 2014). The tag identification number was recorded to identify individual fish. A sample of fish tagged in Fontenelle Reservoir ($n = 50$) was submerged in a 10-m-deep net-pen for 24 h to evaluate short-term tagging and handling mortality. Short-term survival was 98% and short-term tag retention was 100%. We were unable to evaluate short-term mortality and tag retention for fish tagged in the Green River due to the logistics of holding fish for a long period of time; however, we assumed that survival rates were similar to those of reservoir-tagged fish since we used identical tagging methods. Tagged fish were released as close as possible to capture locations, and all release locations were georeferenced using a GPS unit.

We sought to identify the movement dynamics of both adfluvial and fluvial fish; therefore, we allocated radio tags to Burbot in Fontenelle Reservoir and the upper Green River. Burbot in Fontenelle Reservoir were collected using trammel nets in late November 2017. Adfluvial Burbot are known to stage near river mouths prior to migrating upstream for spawning (McPhail and Paragamian 2000). For that reason, trammel netting focused on the upstream portion of the reservoir to improve the probability that a tagged fish was adfluvial. Only large Burbot (>550 mm) were chosen for radio transmitter implantation to increase the chance that tagged Burbot were mature (Klein et al. 2016). Additionally, Burbot in the upper Green River were collected for radio transmitter implantation in August 2017 and November 2018. Riverine Burbot were collected using the methods used to collect fish for PIT tag implantation.

Burbot selected for transmitter implantation were anesthetized before TL (mm) and weight (g) were recorded. Fish were placed in a supine position, and individually coded MCFT2-3EM radio transmitters (Lotek Wireless, Newmarket, Ontario) were implanted into a 1–2-cm incision in the peritoneal cavity (Jakober et al. 1998). Transmitters were programmed to 150.570 MHz, with a 5.0-s burst interval. Minimum battery life for transmitters was 250 d. The antenna exited the body wall using a shielded-needle technique (Ross and Kleiner 1982). Incisions were closed with two to three interrupted sutures. Tag weight (10 g) was less than 3% of total fish weight (Zale et al. 2005) and surgeries were kept under 10 min in duration to minimize stress on the fish. Prior to release, fish were allowed to recover in aerated live wells until they regained equilibrium and responded to touch stimulus (>20 min). Fish were released as close as possible to their original capture location.

Burbot radio-tagged in summer–autumn 2017 were tracked on foot and using fixed-wing aircraft from October 2017 to February 2018, and Burbot radio-tagged in 2018 were tracked from November 2018 to March 2019 using similar methods. Based on PIT tag movement data from 2016 and 2017, this period likely coincided with the Burbot spawning season. Mobile tracking equipment consisted of a portable three-element Yagi antenna in conjunction with a Lotek SRX 800 receiver modified for portability. Antenna error was measured using methods similar to those described by Simpkins and Hubert (1998). Tags were placed underwater and tracked by an observer possessing no knowledge of tag location at various distances from the tag. Error was measured as the distance between a tag's true location and its estimated location. Location error was 1.1 m (SE = 0.2) at 10 m to the radio transmitter and decreased to 0.6 m (SE = 0.1) at 5.0 m. Tracking commenced at the uppermost section of the study area (RKM 125) in a downstream direction. Over time, this area was reduced to include the Green River from 57 km upstream of Fontenelle Reservoir (RKM 75.6) to Fontenelle Dam (RKM 0), as all tagged Burbot remained in that area. Foot-based tracking terminated at the mouth of the upper Green River (RKM 18.6), whereas aircraft-based methods tracked fish from Fontenelle Dam and the upper Green River on a bi-monthly basis (RKM 0–125). Aircraft-based telemetry accuracy was assessed by comparison with known-location radio transmitters. Aircraft detections were less accurate than foot-based detections, and error averaged 68 m (SE = 43). Fish that were located via aerial tracking were later located from the ground to improve accuracy. Once a fish was detected, its location in the river channel was recorded and georeferenced using a GPS unit. Temperature data for the Green River were collected using a U.S. Geological Survey monitoring station located 200 m upstream of the PIT antenna array.

Data analysis.— The initial release locations of fish tagged with PIT tags were uploaded into ArcMap version 10 (Environmental Systems Research Institute, Redlands, California) for analysis. Movement distance was expressed for each detected fish as the total distance between initial release location and the PIT antenna (Muhlfeld and Marotz 2011; Dobos et al. 2016). Distances and timing of movements were summarized by tagging location (i.e., river or reservoir). To avoid the potential influence of behavior (e.g., foraging) on movement data, detections of PIT-tagged fish were classified as migratory if individuals were detected once during a 24-h period or longer before being detected.

Movement of Burbot tagged with radio transmitters was summarized based on the extent of movement and daily movement rate. Extent of movement was defined as the difference between the initial release location of a fish and the farthest upstream or downstream redetections of that individual throughout the study period (Langhurst and Schoenike 1990). Daily movement rate was calculated as the total distance moved divided by the number of days between subsequent detections (Dobos et al. 2016).

Upstream movement was expressed as a positive value and downstream movements were expressed as negative values. Movements were summarized for Burbot during the spawning period. Prespawn and spawning periods were defined based on observed movement patterns in the study system and were considered to occur during the period between river ice-up and the onset of low-elevation runoff (December–March). We estimated that a Burbot had returned to its prespawn location (1) once it moved from the river to the reservoir (for adfluvial fish) or (2) once it returned to the general area of its first detection (for fluvial fish).

A kernel density estimator was used to examine the proportional use of the upper Green River by radio-tagged Burbot during the spawning season (Vokoun 2003). Histograms of detections along the upper Green River were used to obtain the density estimate. Areas of high Burbot use were illustrated by peaks in the utilization distribution and indicate potential spawning locations of Burbot. The univariate kernel density estimator was defined as

$$f(x) = \frac{1}{nh}\sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right),$$

where h is the bandwidth and $K(x)$ is the Gaussian kernel function (Vokoun 2003; Vokoun and Rabeni 2005). The appropriate bandwidth was selected using a Sheather–Jones plug-in method (Jones et al. 1996). Kernel estimates were calculated for the entirety of the Burbot spawning season in 2017 and 2018.

RESULTS

In total, 875 Burbot were implanted with PIT tags. Of these, 421 were tagged in the Green River ($n_{2016} = 280$; $n_{2017} = 141$) and 454 were tagged in Fontenelle Reservoir ($n_{2016} = 237$; $n_{2017} = 217$). Fish tagged in the Green River varied in TL from 200 to 633 mm (mean ± SD = 377 ± 90 mm TL), and fish tagged in Fontenelle Reservoir varied in TL from 282 to 985 mm (535 ± 146 mm TL; Figure 2). Of the fish tagged in the upper Green River, 81 were detected moving downstream toward Fontenelle Reservoir during the spawning period ($n_{2016} = 37$; $n_{2017} = 44$). Detected river-tagged fish varied in TL from 230 to 618 mm (382 ± 71 mm TL; Figure 2). In total, 59 of the Burbot tagged in Fontenelle Reservoir were detected at the PIT antenna ($n_{2016} = 37$; $n_{2017} = 22$). Detected reservoir-tagged Burbot varied in TL from 414 to 850 mm (617 ± 114 mm TL). Lengths of Burbot detected in the Green River were skewed toward larger length-classes compared to the length distribution of all tagged fish.

Movements of Burbot PIT-tagged in the Green River corresponded with water temperatures reaching 0°C (Figure 3). Initial detections of river-tagged fish began in late November, and detections peaked in early to mid-December. Of the detected river-tagged fish, 54% were detected moving back upstream. Mean time spent downstream of the antenna was 30 d (SE = 21). Detections of Burbot tagged in Fontenelle Reservoir moving upstream were highly synchronized. Detections primarily occurred during the last 2 weeks of December in both 2016 and 2017. Like Burbot tagged in the river, movements of fish tagged in the reservoir primarily occurred once water temperatures reached 0°C. Mean time spent upstream of the PIT antenna for reservoir-tagged Burbot was 21 d (SE = 14).

Approximately 31% of the Burbot tagged within 12 km upstream of the antenna were detected moving downstream (Figure 4). Detected fish that were tagged in this section of river accounted for 79% of the total number of detections for river-tagged fish. Of the total detections of river-tagged fish, 96% traveled <24 km downstream from their initial tagging location. The maximum distance traveled downstream by a PIT-tagged Burbot was 35 km.

In total, 40 radio transmitters were implanted in Burbot during 2017. Eighteen transmitters were implanted in Burbot from the upper Green River in August 2017, and 22 transmitters were implanted in Burbot in Fontenelle Reservoir during November 2017. In November 2018, an additional 13 Burbot were radio-tagged in the upper Green River. Total length of fish radio-tagged in the Green River varied from 430 to 711 mm (mean ± SD = 509 ± 71 mm TL) in 2017 and from 421 to 612 mm (512 ± 55 mm TL) in 2018. Total length of radio-tagged fish in Fontenelle Reservoir varied from 560 to 905 mm (713 ± 100 mm TL). No detections were made for river-tagged fish in 2017 due to high rates of tag malfunction (>60%) and mortality, but fish radio-tagged in 2018 were detected a total of 110 times (Figure 5). Of 22 fish tagged in Fontenelle Reservoir, 10 were detected in the Green River and 1 was detected in the mouth of Fontenelle Creek, a tributary to Fontenelle Reservoir. The remaining 11 fish were not detected due to attenuation caused by the depth of the reservoir or transmitter malfunction. In total, 191 detections were made on Burbot radio-tagged in Fontenelle Reservoir (Figure 5). Similar to movement of PIT-tagged fish, movement of reservoir-tagged Burbot into the Green River was synchronized. All fish entered the Green River from December 10 to December 16 after river temperature dropped to 0°C. Once in the Green River, movement patterns were variable among individual adfluvial Burbot. Maximum upstream distance traveled by a fish from its release site in Fontenelle Reservoir was 13.2 km (Figure 5). However, maximum upstream distance traveled from the mouth of the river was only 5.8 km. Mean daily movement rates for adfluvial Burbot varied from −30 to 142 m/d (mean ± SD = 67 ± 59 m/d). Similar to adfluvial Burbot, river-tagged Burbot movement rates were highly variable; however, 11 of 13 tagged fish moved downstream in

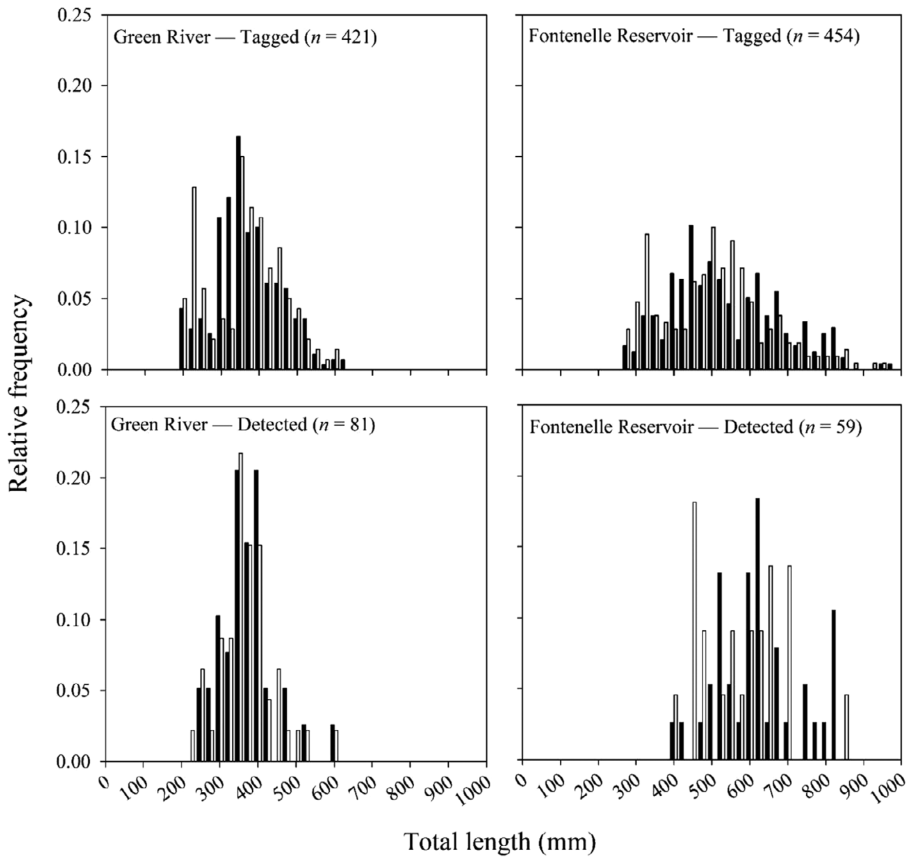

FIGURE 2. Length frequency distributions of Burbot PIT-tagged in the upper Green River and Fontenelle Reservoir, Wyoming, and Burbot detected at a PIT antenna located near the mouth of the upper Green River in 2016 (black bars) and 2017 (white bars).

relative synchrony during the spawning period and these movements coincided with river ice-up. Mean daily movement rates varied from −612 to 97 m/d (4 ± 198 m/d). Maximum downstream distance traveled by a river-tagged Burbot was 17.7 km. Kernel density estimates suggested a high probability of both fluvial and adfluvial Burbot use between RKM 19 and RKM 26 during the spawning period (Figure 6). Additionally, detection data suggested high fluvial Burbot use near RKM 38–39 during the spawning period.

DISCUSSION

Burbot movement dynamics have been studied throughout the species' distribution (Evenson 1993; Carl 1995; Arndt and Hutchinson 2000; Schram 2000; Paragamian et al. 2005; Dillen et al. 2008; Dunnigan and Sinclair 2008; Paragamian and Wakkinen 2008). Although patterns in movement vary based on their geographic location, prior research suggests that movement is generally highest during the prespawn and spawning periods (i.e., winter). In the Tanana River, Alaska, Burbot movement was most prevalent during winter months and coincided with river ice-up (Evenson 1993). Similarly, movement of radio-tagged Burbot in the Kootenai River, Idaho, peaked during winter months when water temperatures dropped below 4°C (Paragamian and Wakkinen 2008). Both PIT- and radio-tagged Burbot in our study exhibited peak movement during the spawning season. In fact, movements were almost entirely observed after water temperatures reached 0°C, when both the upper Green River and Fontenelle Reservoir were covered in ice. The relationship between Burbot spawning movements and temperature in our study was similar to that reported for other systems, but the timing of movements and the suspected spawning period were dissimilar. Specifically, Cott et al. (2013) reported little variation in the timing of spawning in 24 lacustrine Burbot populations throughout Canada, regardless of differences in environmental conditions (e.g., duration of ice cover). Spawning generally occurred during the first 3 weeks of February in these populations. In our study, Burbot in the Green River likely spawned primarily in January. Movement data suggest that Burbot conducted prespawn movements synchronously in mid-

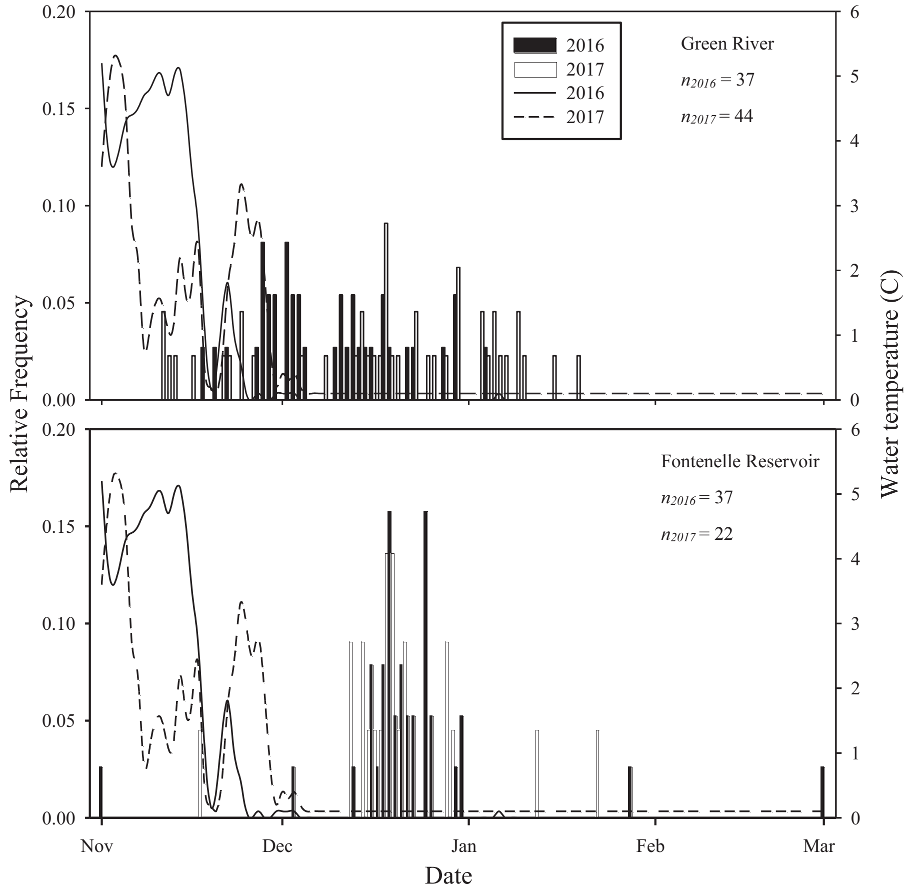

FIGURE 3. Histograms depicting the timing of initial detections of Burbot at a stationary PIT antenna array located 7 km upstream of Fontenelle Reservoir for fish that were PIT-tagged in Fontenelle Reservoir and the upper Green River, Wyoming. Frequency of detections and mean daily water temperature (°C) for the upper Green River in 2016 (black bars; solid line) and 2017 (white bars; dashed line) are provided. Total number of individuals detected is provided for 2016 and 2017.

December and returned to their prespawn locations after a period consistent with other populations reviewed by Cott et al. (2013). This dissimilarity in movement timing may be the result of an earlier onset of freezing water temperatures in the GRB. In addition, Burbot movements have not been previously described for areas outside of their native distribution, so comparisons with other populations may be somewhat tenuous.

Adfluvial life histories are common in Burbot populations (Sorokin 1971); given the lentic origin of Burbot illegally introduced in the Green River (Boysen Reservoir, Wyoming; Underwood et al. 2016), it is not surprising that they are exhibiting historic adfluvial life history traits in their adopted river system. Burbot have been shown to exhibit high ecological plasticity, which may explain their success in the Green River system. For example, hatchery-reared, lake-origin Burbot adopted riverine environments over lacustrine environments when stocked into the Kootenai River, Idaho (Hardy et al. 2015). Our study suggests that a substantial portion of the Burbot population in Fontenelle Reservoir exhibits an adfluvial life history. Of the total number of fish PIT-tagged in Fontenelle Reservoir, 10–15% were detected in the upper Green River throughout the spawning season depending on the year of the study. Additionally, only mature fish seemed to be making migrations based on length distribution of detected fish and the relative size of fish maturity in the GRB (Klein et al. 2016; Brauer et al. 2019). Observation of mature fish undertaking migration provides further evidence that these movements are spawning related.

The distances traveled by adfluvial fish in our study were different from those of other adfluvial populations of Burbot. For example, Schram (2000) documented upstream migrations of Burbot over 50 km from Lake Superior, Wisconsin, into various tributaries. Fluvial Burbot also exhibit long migrations, sometimes exceeding 200 km (Evenson 1993). In our study, radio-tagged adfluvial Burbot traveled a maximum of 6 km into the Green River, with most fish staying within 2 km of Fontenelle

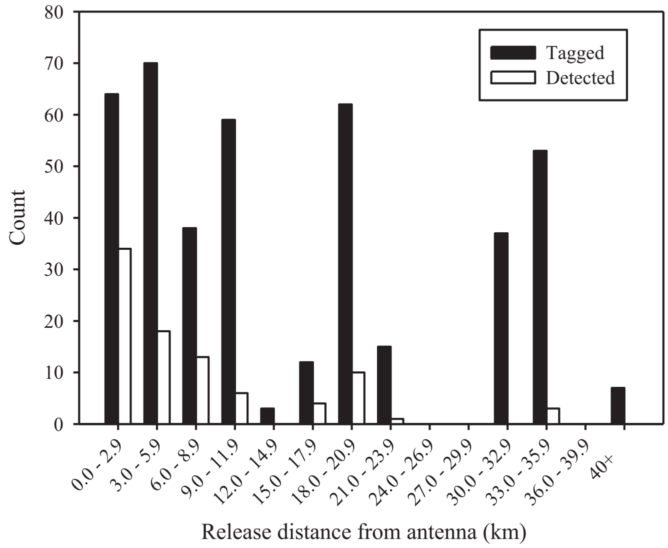

FIGURE 4. Histogram depicting total number of Burbot PIT-tagged in the upper Green River (black bars) and total number of Burbot redetected at the PIT antenna (white bars) in relation to individual fish tagging/release site distance (km) from the PIT antenna. Data from 2016 and 2017 are included.

Reservoir. Upstream movements generally occurred over a short time period, and fish remained sedentary upon reaching suspected spawning areas. Conversely, Burbot that were radio-tagged in the upper Green River exhibited downstream movements to the same general areas occupied by adfluvial fish during the spawning period. Similar to adfluvial fish movements, downstream movements by fluvial fish occurred over a short time period and fish remained sedentary upon reaching spawning areas. River-tagged fish were then observed returning to their original tagging locations after the spawning period. Habitat used by Burbot within 2 km of Fontenelle Reservoir was characterized by low-velocity runs and pools with coarse substrate and proximity to alluvium bluff banks. Habitats used by Burbot over 2 km upstream of the reservoir were primarily low-velocity runs located off the main channel. The types of habitats used by Burbot during the winter are consistent with other studies of habitat use by Burbot both within and outside the GRB (Paragamian 2000; Klein et al. 2015b).

Our PIT tag and radiotelemetry data suggest that fluvial Burbot travel downstream to spawning sites used by adfluvial Burbot and return upstream after the spawning period. While we have no direct evidence of spawning, other Burbot populations have exhibited extensive downstream movements to reach spawning sites (Robins and Deubler 1955; Evenson 1993) and Burbot in the Green River may be exhibiting similar, albeit shorter, movement patterns. From a management perspective, short Burbot migration distances may benefit a suppression program because spawning is likely occurring in a relatively small section of the upper Green River. Targeting the area within 8 km of Fontenelle Reservoir may improve the overall efficiency of

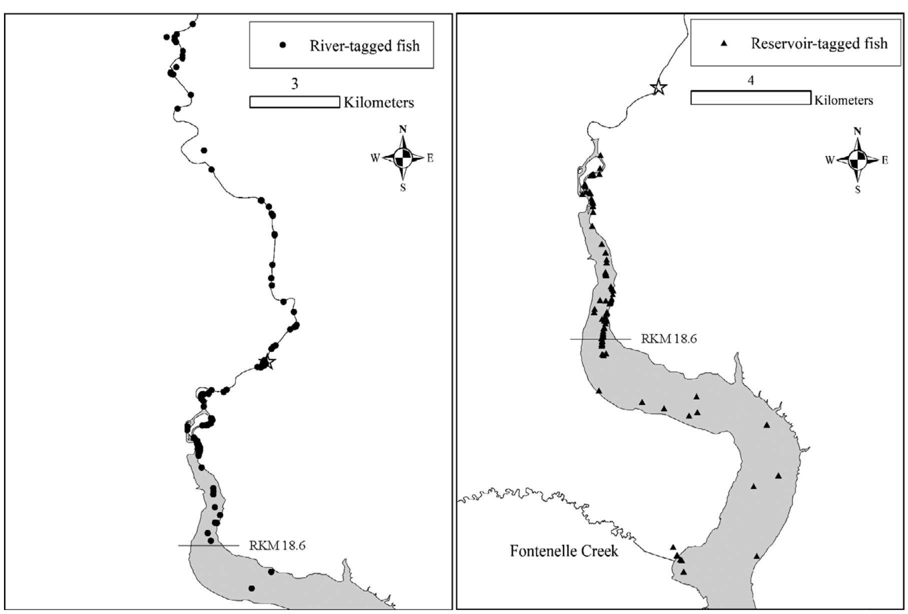

FIGURE 5. Detection of Burbot radio-tagged in the upper Green River and Fontenelle Reservoir during winter 2017–2018 and 2018–2019. The horizontal line represents the mouth of the upper Green River (RKM 18.6) from December 2017 to February 2018 and from November 2018 to March 2019. The river mouth is within the inundation area of the reservoir, though it is rarely inundated. The location of the PIT antenna array is indicated by a star.

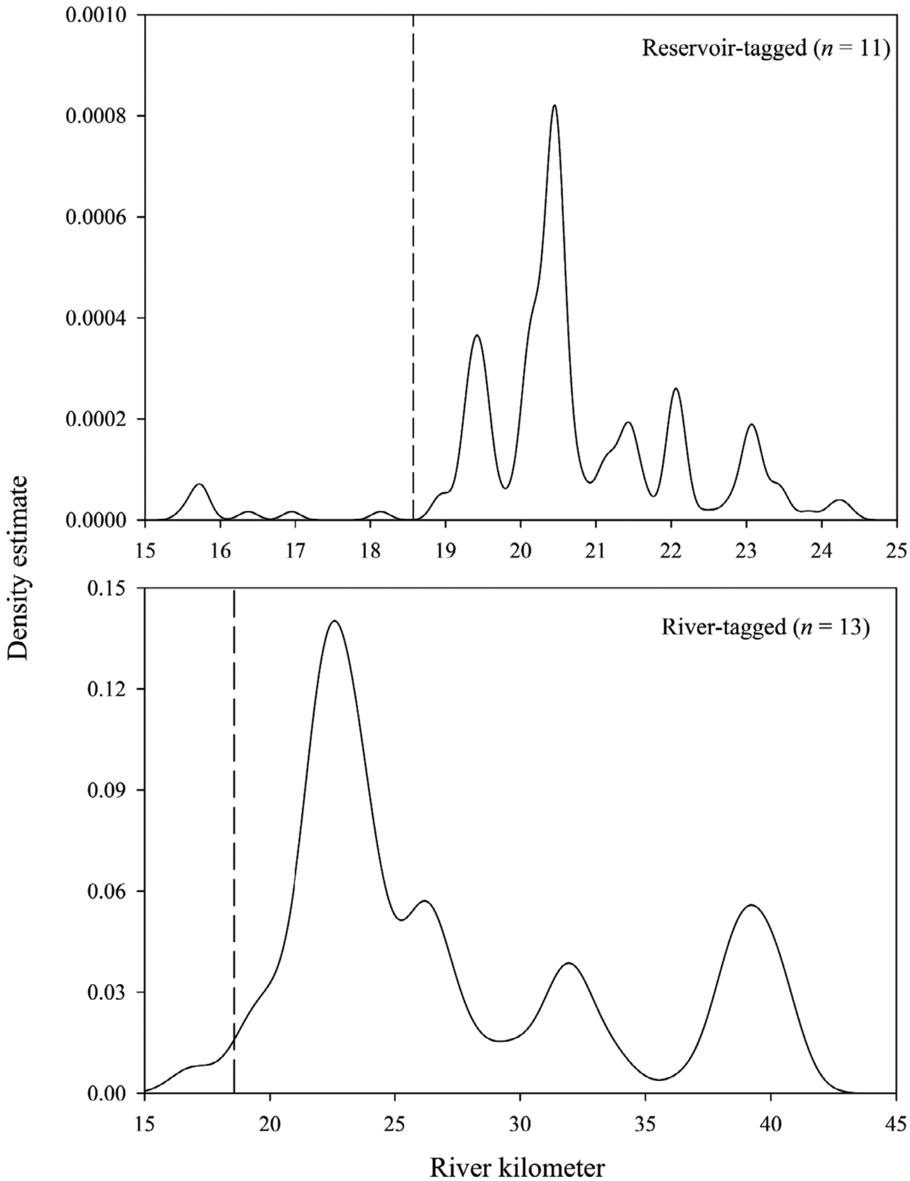

FIGURE 6. Kernel density estimates for winter detections of radio-tagged Burbot in the upper Green River and Fontenelle Reservoir, Wyoming, in 2017–2018 and 2018–2019. The vertical dashed line (RKM 18.6) represents the mouth of the upper Green River. The number of Burbot detected is included.

removal efforts. However, mechanical removal of Burbot during the spawning season may be difficult and dangerous since the Green River is covered in ice during that period. Despite the inherent difficulties brought on by ice cover, this section of the Green River could also be targeted during the spring months after the spawning season. Prior research suggests that increases in mortality of juvenile Burbot have the greatest effect on reducing Burbot population growth (Klein et al. 2016; Brauer et al. 2019). Beard et al. (2017) observed low levels of dispersion for juvenile Burbot stocked in Deep Creek, Idaho. If wild juvenile Burbot exhibit similar movement patterns in the Green River, targeting these sites after ice-off may increase the efficiency of removal efforts on juvenile age-classes.

The objective of this study was to identify the movement dynamics of Burbot in the upper GRB. Due to a mixture of high tag failure rates (>60%) and suspected mortality, we were unable to track fish that were radio-tagged in the Green River in 2017. High tag failure rates in 2017 were due to faulty components in radio tags, causing frequency drift (Lotek, personal communication). Of the five suspected mortalities, three tags were located above the high-water mark. Two of these tags were found near North American river otter *Lontra canadensis* latrine sites, and one tag was found at the base of a large tree containing a western osprey *Pandion haliaetus* nest. The remaining two unconfirmed mortalities were considered dead due to lack of movement over a 5-month period and because they were in areas of river that were not favorable for Burbot (i.e., very shallow depth). The high mortality rate of radio-tagged Burbot in the Green River may be a result of the riverine fish being exposed to high water temperatures during tagging (13–15°C). Tags that were located above the high-water mark may be the result of direct predation or scavenging of dead Burbot by terrestrial and avian predators. Despite difficulties tracking fish in 2017–2018, Burbot that were radio-tagged in November 2018 were successfully tracked into 2019 to fill this data gap.

This study provides critical insight into the movement dynamics of Burbot in the upper Green River system. Given the potential of Burbot to alter the food web in the Green River, understanding their movement dynamics will both increase the effectiveness of suppression efforts and provide insight on potential interactions of Burbot with important sport fishes. The results of this research suggest that a substantial portion of the Burbot population in the upper Green River exhibits an adfluvial life history and that the same general spawning areas used by adfluvial fish are also used by fluvial Burbot. Fish movements are generally short in distance, with the majority of suspected spawning locations occurring in close proximity to Fontenelle Reservoir, and those locations may serve as targets for suppression efforts. However, it is still relatively unknown how important this spawning area is to the Green River Burbot population as a whole and that question may warrant further investigation. This research also provides insight into the ecology of Burbot outside of Wyoming and may assist in the management of imperiled Burbot populations throughout their distribution by further demonstrating the variability in Burbot ecology among populations.

ACKNOWLEDGMENTS

We thank K. Brauer, G. Briley, M. Miner, R. Keith, and J. Walrath for their assistance with data collection. We also thank the landowners along the upper Green River for their cooperation with this research. S. Stephenson and three anonymous reviewers provided helpful comments on an earlier version of the manuscript. Funding was provided by the WGFD. Additional support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, Idaho Department of Fish and Game, and Wildlife Management Institute. This project was conducted under University of Idaho Institutional Animal Care and Use Committee Protocol 2016-02. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. There is no conflict of interest declared in this article.

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