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Burbot (*Lota lota*) exhibit plasticity in life-history traits in a small drainage at the southwestern-most extent of the species' native range

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Summary

Little is known about the life-history traits exhibited by burbot (*Lota lota*) throughout their circumpolar range. Monitoring burbot movements between lentic and lotic habits and collection of demographic data (length, age, sex, and maturity) were used to answer the following questions in the Torrey Creek drainage of west-central Wyoming, USA: (a) is there plasticity in the life-history traits of the burbot population, (b) do Trail Lake origin and Torrey Creek origin burbot interchange during the spawning period, and (c) is there a difference in growth and age at sexual maturity between burbot captured in Trail Lake and Torrey Creek? Results indicated that burbot in Trail Lake and Torrey Creek exhibit plasticity in their life history traits. Directional movement of PIT-tagged burbot in Trail Lake and Torrey Creek was monitored nearly continuously by tandem stream-width antennas. Thirty-five percent of lentic-origin burbot migrated upstream into Torrey Creek, and 11% of lotic-origin burbot migrated downstream of the antennas near the Torrey Creek inlet to Trail Lake. Migratory activity of burbot was highest during the late winter and early spring at a time that coincided with spawning. Additionally, Torrey Creek-origin burbot were smaller and younger than Trail Lake-origin burbot. In addition to documenting migration, the sampling of small, sexually mature burbot in Torrey Creek suggests that stream-resident burbot reach maturity earlier than adfluvial and lacustrine burbot in Trail Lake. Furthermore, high catch rates of age-0 burbot indicate that Torrey Creek upstream from Trail Lake provides nursery habitat to the burbot population. Life history trait plasticity and spawning and nursery habitats documented in this study should be considered when selecting conservation actions for this unique burbot population.

KEYWORDS
burbot, life-history, *Lota lota*, PIT tag

1 | INTRODUCTION

Burbot (*Lota lota*) is the only freshwater representative of the cod family (*Gadidae*) and one of two freshwater fish species (along with northern pike [*Esox Lucius*]) with a circumpolar distribution across North America, Europe, and Asia (McPhail & Paragamian, 2000; Figure 1). Plasticity in life-history traits and physiological adaptations allow the species to persist in a variety of lentic and lotic environments (Brauer et al., 2019, 2020; Evenson, 1989, 1990b, 1993; Hardy et al., 2015; Holker et al., 2004; Jude et al., 2013; Klein et al., 2016). Burbot are top predators in freshwater ecosystems, with a diet that consists primarily of fish and aquatic invertebrates (Bailey, 1972; Bjorn, 1940; Chen, 1969; Cott et al., 2011; Hewson, 1955; Jacobs et al., 2010; McBaine et al., 2018;

FIGURE 1 Illustration of a burbot by Joseph Tomelleri

Miller, 1970a, 1970b; Williams, 1959). Spawning predominantly occurs in winter or early spring over sand, gravel, or cobble substrate (McPhail & Paragamian, 2000). Burbot are cultural resources to indigenous peoples in North America, support commercial fisheries in Eurasia, and are targeted by recreational anglers worldwide (Ahrens & Korman, 2002; Evenson, 1989; Hardy & Paragamian, 2013; Hubert et al., 2008; Quinn, 2000; Stapanian et al., 2010). The largest burbot recognized by The International Game Fish Association is an 11.4 kg individual captured in Lake Diefenbaker, Saskatchewan, Canada, although variability in sizes exist within and among populations.

Many burbot populations are declining as the result of exploitation, pollution, habitat change, and competition with invasive species (Ahrens & Korman, 2002; Bernard et al., 1993; Paragamian et al., 2000; Stapanian et al., 2010). Understanding the factors and habitats that affect different life-history traits is important for mitigating population declines and developing species-specific management actions. For example, movement studies of residential and migratory burbot throughout the Tanana River basin, Alaska, led to management of the fishery as one stock despite differences in burbot density and size structure that indicated the existence of multiple life-history traits (Evenson, 1989, 1990b, 1993). Information on burbot life-history traits within a population may also help managers suppress burbot outside of their native range. Recurrent use of a spawning area in the upper Green River of Wyoming indicated future suppression efforts may be effective for both fluvial and adfluvial burbot (Brauer et al., 2020). Differences in population demographics (i.e., growth, maturity, and mortality) also indicated different suppression strategies are necessary for non-native burbot in lentic and lotic habitats in the Green River drainage (Brauer et al., 2019; Klein et al., 2016).

Within North America, burbot of the Wind River basin occupy the southwestern-most portion of the species' native range, and are designated as a Species of Greatest Conservation Need in Wyoming (Wyoming Game & Fish Department, 2017). Of the four Wind River basin burbot populations, three occupy lentic and lotic habitat within discrete tributary drainages (Torrey Creek, Dinwoody Creek, and Bull Lake Creek), and the other occupies a main-stem reservoir (Boysen Reservoir). Exploitation, entrainment in canals, silt deposition, reservoir water-level variation, and habitat fragmentation by dams are considered possible threats to burbot in the Wind River basin, and were previously identified as high-priority research needs (Hubert et al., 2008; Krueger & Hubert, 1997). A considerable amount of research has focused on threats to burbot in the Wind River basin since 2011. Subsequent studies determined that exploitation is a probable threat to burbot in the Dinwoody Creek drainage, but not in the Bull Lake Creek or Torrey Creek drainages (Lewandoski et al., 2017). Entrainment in canals and habitat fragmentation by dams were also determined to pose little threat to basin-wide burbot populations (Hooley-Underwood et al., 2018; Underwood et al., 2016).

Although recent research has given managers insight on potential threats, more information is also needed regarding the source-sink dynamics of burbot within the Wind River basin (Hubert et al., 2008). Understanding the role of spawning locations and the magnitude of natural recruitment that maintain various populations is especially important for directing population conservation and management decisions (Hubert et al., 2008). Research conducted in the 1930s, 1950s, and 1960s suggested a variety of natural recruitment strategies are utilized by burbot within the Torrey Creek drainage. More specifically, it was hypothesized that lake-resident burbot migrated into Torrey Creek to spawn; however, this claim was never verified (Bjorn, 1940; Hagan, 1952; Williams, 1959). Conversely, lacustrine spawning activity of burbot has been documented within the drainage in Ring Lake (Miller, 1970b). It was, however, found that lacustrine burbot grow to a larger size than burbot in Torrey Creek (Miller, 1970a, 1970b). To date, the understanding of burbot life history in the Torrey Creek drainage is poorly understood.

Despite the hypotheses posited by Bjorn (1940), Hagan (1952), Williams (1959), and Miller (1970a, 1970b) – that burbot display adfluvial, lake-resident, and stream-resident life history traits – no additional research has been conducted to explicitly determine the strategies used by burbot for natural recruitment in the Torrey Creek drainage. Anecdotal evidence suggested that connectivity exists between lake- and stream-resident burbot, but that differences in demographics within the population (i.e., growth and age at sexual maturity) also exist. If interchange of individuals occurs between the stream and lakes, it is important to establish the level of connectivity and influence of life histories on the burbot population within the drainage so that necessary habitats can be protected (e.g., spawning and nursery areas, migratory routes). We address the following questions to better understand the life-history traits of burbot: (a) is there plasticity in the life-history traits of the burbot population in the Torrey Creek drainage, (b) do Trail Lake origin and Torrey Creek origin burbot interchange during the spawning period, and (c) is there a difference in growth and age at sexual maturity between burbot in Trail Lake and Torrey Creek?

2 | MATERIALS AND METHODS

2.1 | Study system

The Torrey Creek drainage originates in the Wind River Mountain Range and flows north into the Wind River in northwest Wyoming (Figures 2 and 3). Burbot occupy three glacially formed alpine lakes (Torrey, Ring, and Trail) and four reaches of Torrey Creek (approximately 13 km) within the drainage (2,045–2,269 m above sea level). The four reaches of Torrey Creek that burbot occupy include approximately 7.7 km between Torrey Lake and the confluence with the Wind River, 0.2 km between Torrey and Ring lakes, 1.3 km between

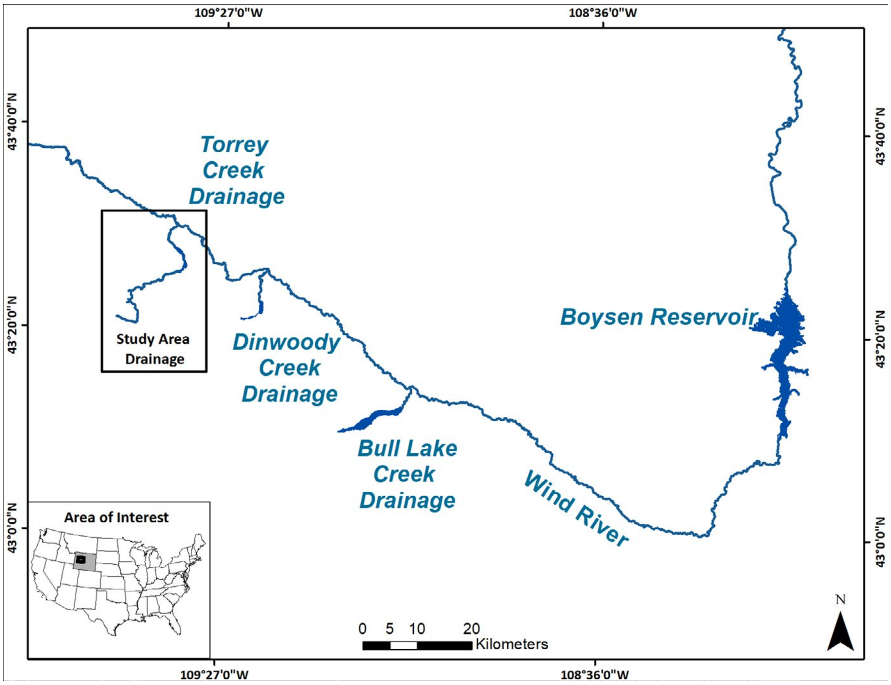

FIGURE 2 Distribution of the four primary burbot populations (Boysen Reservoir and the Torrey, Dinwoody, and Bull Lake creek drainages) within the Wind River basin, Wyoming

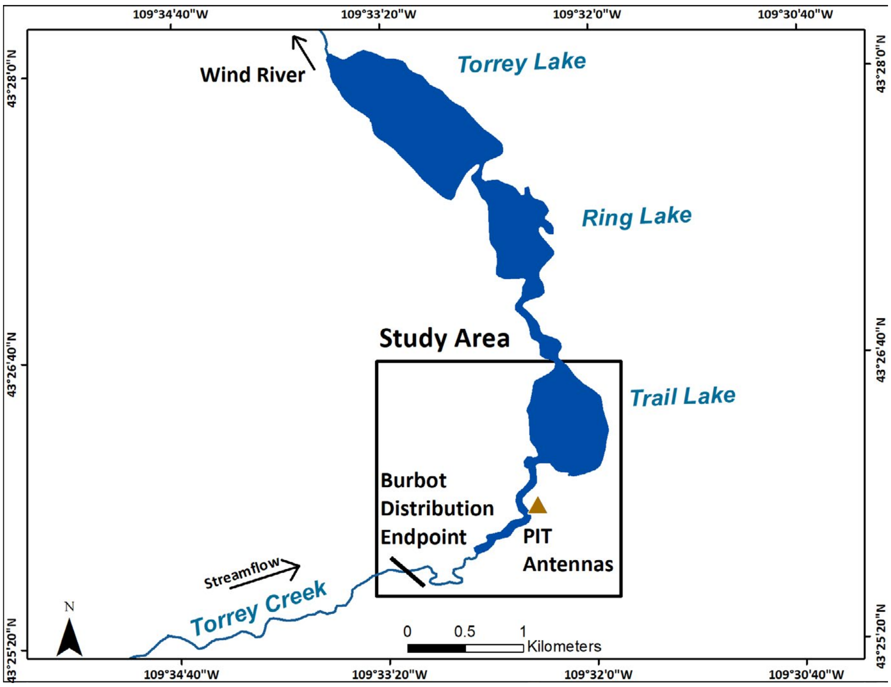

FIGURE 3 The study area (enclosed within the black square downstream of the perpendicular black bar) of the Torrey Creek drainage, Wyoming

Ring and Trail lakes, and 3.8 km upstream from Trail Lake. Burbot can move unimpeded between Torrey Lake and the first 3.8 km of Torrey Creek upstream from Trail Lake; however, cascading stream reaches downstream from Torrey Lake most likely prevent upstream movement (Hubert et al., 2008). Steep gradient, swift current velocity, and lack of pool habitat are probable causes for the absence of burbot in Torrey Creek farther than 3.8 km upstream from Trail Lake. This study focused only on burbot within Trail Lake and the 3.8 km portion of Torrey Creek immediately upstream of the lake confluence (Figure 3).

2.2 | Fish sampling and tagging

Sampling of burbot for passive integrated transponder (PIT) tagging in Torrey Creek and Trail Lake occurred monthly from June through October 2013. Sampling also occurred in October 2014 to obtain otoliths for aging and examine gonads to determine sex and maturity. Torrey Creek was sampled with either a cataraft-mounted or a bank electrofishing unit depending on flow conditions. Lotic sampling occurred primarily upstream (between 0.13 and 0.40 km) of the upper PIT antenna after comprehensive sampling of 1.1-km between the lake confluence and the array yielded few burbot (*N* = 3). Sampling of burbot in near-shore habitat in Trail Lake was conducted at night using shoreline boat electrofishing once-per-month from June through September 2013; one pass was completed along the circumference of the lake (3.3 km) during each event. Shoreline electrofishing was not conducted in October 2013 or October 2014 because of a malfunctioning electrofishing boat. All electrofishing throughout the study was conducted using a Smith-Root VVP-15B Electrofisher. Burbot were sampled in offshore habitat with trammel nets and baited cod traps in October 2013 and 2014. Trammel nets were 48.8-m long and 1.8-m deep with outer panels of 25.4-cm bar mesh and inner panels of 2.5-cm bar mesh. All trammel nets were set perpendicular to shorelines (littoral sets) or prominent underwater features (benthic sets) and allowed to fish overnight. Circular cod traps had 2.5-cm bar mesh and measured 60-cm tall with a base diameter of 96-cm and a top diameter of 66-cm. Cod traps were baited with trammel net bycatch mortalities (primarily white sucker *Catostomus commersonii*) and allowed to fish overnight in benthic habitat before retrieval.

All burbot ≥75 mm were scanned for the presence of a preexisting PIT tag with an Allflex RS200B Compact Reader, measured to the nearest millimeter (total length), and weighed to the nearest gram. One 12-mm half-duplex (HDX) PIT tag (Oregon RFID; 11.5 mm long, 2.1 mm wide, 0.1 g in air) was injected into the peritoneal cavity of all burbot ≥75 mm sampled in 2013 using a syringe implanter (Ashton et al., 2014). Burbot <75 mm were too small to be tagged and were enumerated and released during 2013 sampling; however, all individuals sampled during the final October 2014 sampling were sacrificed for age, sex, and maturity determination.

2.3 | PIT antenna specifications

Burbot movements within the study area were monitored by an autonomous PIT tag antenna array (HDX Multiplexor; Oregon RFID) between mid-September 2013 and mid-October 2014. Although preferential for quantifying burbot movements between lentic and lotic habitat, the PIT antenna array was not installed at the confluence between Trail Lake and Torrey Creek because of the presence of multiple lake inlets associated with a braided stream channel. The PIT antenna array was installed upstream from the braided stream channel, 1.1-km upstream from the Trail Lake inlet. Two stream-width antennas were installed, separated by 25 m. A pass-over antenna array configuration was selected because of substantial recreational use throughout the study area, wide stream channel at the installation site, and low-flow conditions during the study period (Connolly et al., 2008; Greenberg & Giller, 2000). To increase antenna stability and reduce the need for frequent tuning, both antennas were shrouded within 19.1 mm polyvinyl chloride piping in a rectangular shape (Connolly et al., 2008). Each antenna was roughly 26.5-m long and 0.7-m wide, and consisted of a double coil of 7/0 AWG speaker power cable. The antennas were secured to the gravel substrate with wooden dowel rods connected by waxed cording to reduce interference and noise levels generated by close proximity of ferric metal loops (Bond et al., 2007). The PIT array power supply (two 12 V deep-cycle batteries connected in series) was serviced weekly; facilitating the opportunity to manually tune each antenna and download detection data. Although antenna efficiency was not measured, a PIT tag was often passed over both antennas at the stream surface during the weekly services to confirm the array was functioning properly and successfully detecting tags at maximum distance directly above the antennas.

2.4 | Movement data collection

The autonomous PIT reader was operated nearly continuously from September 11, 2013 to October 6, 2014 to assess seasonal movement within the study area. The PIT reader was configured to document the date, time, antenna number, and unique tag ID of PIT-tagged burbot that passed over the antenna. Based on tagging origin and detections of individual fish at the antennas, upstream and downstream movement was inferred for all detected burbot.

Malfunctions of the PIT reader occurred during the winter and early summer of 2014. From February 3 to 8, 2014, two burbot that were tagged upstream from the PIT array in Torrey Creek were first detected by the downstream antenna, and one burbot that was tagged in Trail Lake downstream from the PIT array was first detected by the upstream antenna. Additionally, one burbot that was detected by the upstream antenna on February 25 was subsequently detected only by the downstream antenna on March 4. These aberrant detection patterns were likely caused by sporadic antenna outages rather than long periods without coverage, as many detections were documented throughout the winter. The reader outages during February 2014 were probably caused by cold temperatures that periodically drained the 12 V battery power source. The early-summer reader malfunction occurred after high flows and debris damaged the PIT reader and dislodged one of the antennas. As a result, no burbot movements were registered from June 6 to June 18, 2014. Additionally, incomplete reader outages, where one of the two antennas was operational, occurred from June 1 to June 6 and June 18 to July 24, 2014; thus, allowing for the detection of migrating fish without the ability to determine directional travel.

2.5 | Growth, maturity, size, and age structure

Sex and maturity were determined and sagittal otoliths were obtained for aging from 41 burbot sampled in Torrey Creek (77–453 mm) and 18 burbot sampled in Trail Lake (290–650 mm) in October 2014. A tricaine methanesulfonate bath was used to anesthetize and euthanize burbot. Sex and maturity were classified by visually examining gonads in the field (Hewson, 1955). Mature male gonads were angular, engorged, and opaque, whereas immature male gonads were similar in shape but smaller and translucent. Mature female gonads were round, vascularized, and contained developing eggs. Immature female gonads were round, lacked vascularization, translucent, and did not contain eggs. Otoliths were prepared and aged in a laboratory using methods similar to Stuby (2008). One otolith from each burbot was embedded into epoxy resin and transversely sectioned through the nucleus using a slow-speed IsoMet saw (Buehler). Otolith sections were affixed to a glass slide with cyanoacrylate glue and polished to remove surface imperfections and improve clarity. A stereoscopic microscope was used to age all burbot otoliths. Two readers without knowledge of fish length or weight independently aged all otoliths, and discrepancies were resolved using a third reader.

A two-sample *t*-test was used to determine statistical differences in: (a) mean length of burbot sampled in near-shore and offshore habitat in Trail Lake; (b) length of mature burbot between Torrey Creek and Trail Lake; (c) length of immature burbot between Torrey Creek and Trail Lake; (d) age of mature burbot between Torrey Creek and Trail Lake; and (e) age of immature burbot between Torrey Creek and Trail Lake. Diagnostic tests (probability plots for normality and Levene's test for equal variance) were used to confirm that data were appropriate for parametric analyses. Minitab Version 18 was used for all statistical analyses, ArcGIS version 10.3.1 was used to create Figures 2 and 3, and SigmaPlot Version 13 was used to create Figures 4–7.

3 | RESULTS

3.1 | Fish sampling and PIT tagging

Forty-six burbot were PIT-tagged and released in Trail Lake (142–790 mm) and 141 burbot were PIT tagged and released in Torrey Creek upstream from Trail Lake (97–392 mm) from June 19 to October 22, 2013. Two burbot were captured and PIT tagged in Torrey Creek downstream from the PIT antenna array, and 139 burbot were captured and PIT tagged in Torrey Creek upstream from the PIT antenna array. First-pass electrofishing catch rate was higher in Torrey Creek (mean = 63.0 burbot/km; 95% CI ±70.3 burbot/km) than Trail Lake (mean = 1.1 burbot/km; 95% CI ±1.6 burbot/km) during June–September 2013 sampling events. Mean length of burbot sampled by electrofishing in near-shore habitat (mean = 207 mm; minimum and maximum = 117–320 mm; $N = 13$) differed from, and was smaller than, the mean length of burbot sampled by cod traps and trammel nets in offshore habitat (mean = 419 mm; minimum and maximum = 287–790 mm; $N = 61$) in Trail Lake ($T = 9.86$, $p < .001$, $df = 46$).

3.2 | Movement

Burbot in the upper Torrey Creek drainage exhibited temporal variation in migration patterns. Seventeen percent of all PIT-tagged burbot ($N = 187$) were detected moving past the PIT antenna array. Thirty-five percent ($N = 16$) of burbot tagged in Trail Lake migrated upstream into Torrey Creek and 11% ($N = 16$) of burbot tagged in Torrey Creek migrated downstream. Only Torrey Creek-origin burbot that were tagged and released upstream from the PIT antenna array were detected: neither of the two Torrey Creek-origin burbot that were tagged and released downstream from the PIT antenna array were detected. The amount of time between first and last detections of Torrey Creek-origin burbot at the PIT antenna array varied from 1 to 209 days (mean = 54 days; $N = 16$). The amount of time between first and last detections of Trail Lake-origin burbot at the PIT antenna array varied from 2 to 118 days (mean = 36 days; $N = 16$). Migratory Trail Lake-origin fish varied in length from 325 to 790 mm while Torrey Creek-origin fish that moved past the PIT antenna array varied in length from 145 to 391 mm. With the exception of three Torrey Creek-origin individuals, both Trail Lake and Torrey Creek-origin burbot initiated migration from late-November through March (Figure 4). Furthermore, the number of unique detections per day indicated that there was substantial and repeated interchange of tagged burbot between Torrey

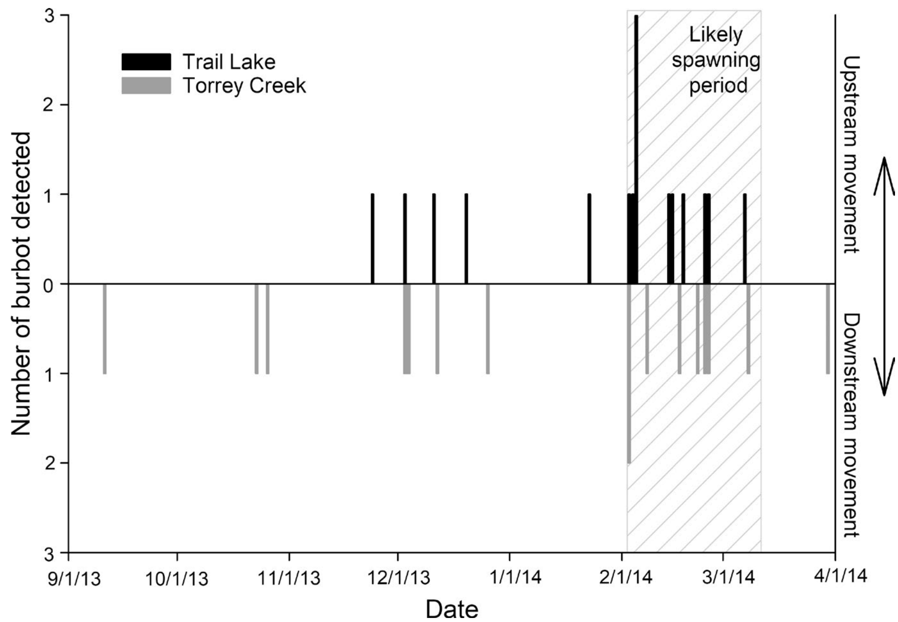

FIGURE 4 Initial detections of Trail Lake-origin burbot (black) and Torrey Creek-origin burbot (grey) at the Torrey Creek PIT antenna array, September 2013–October 2014. Histogram was abridged because no new detections were recorded after April 1, 2014

Creek and Trail Lake throughout the course of the study (Figure 5). Detections at the PIT antenna array occurred from September to June; however the majority of detections occurred from early February through early March with a peak in late February (Figure 5).

3.3 | Growth, maturity, size, and age structure

A higher proportion of smaller and younger fish were sampled in Torrey Creek than Trail Lake (Figures 6 and 7). Of all burbot sampled in Torrey Creek in September and October 2013 ($N = 132$), 64% were ≤97 mm and likely age-0, whereas no age-0 burbot were sampled in Trail Lake. The majority of Torrey Creek burbot sampled in October 2014 were age 0 to age 2 (82%), whereas 100% of Trail Lake burbot were ≥ age 3 (Figure 7). The proportion of mature fish was similar between Torrey Creek (44%; $N = 19$) and Trail Lake (56%; $N = 10$); however, mean length ($T = -4.1$, $p < .01$, $df = 11$) and age ($T = -4.25$, $p < .01$, $df = 11$) of mature female burbot in Torrey Creek differed from, and were less than, mature female burbot in Trail Lake (Tables 1 and 2). Additionally, mean length ($T = -6.04$, $p < .01$, $df = 8$) and age ($T = -3.59$, $p < .01$, $df = 8$) of immature female burbot in Trail Lake differed from, and were greater than, immature female burbot in Torrey Creek (Tables 1 and 2).

4 | DISCUSSION

This study shows that burbot exhibit plasticity in life-history traits in the Torrey Creek drainage. Documentation of interchange between

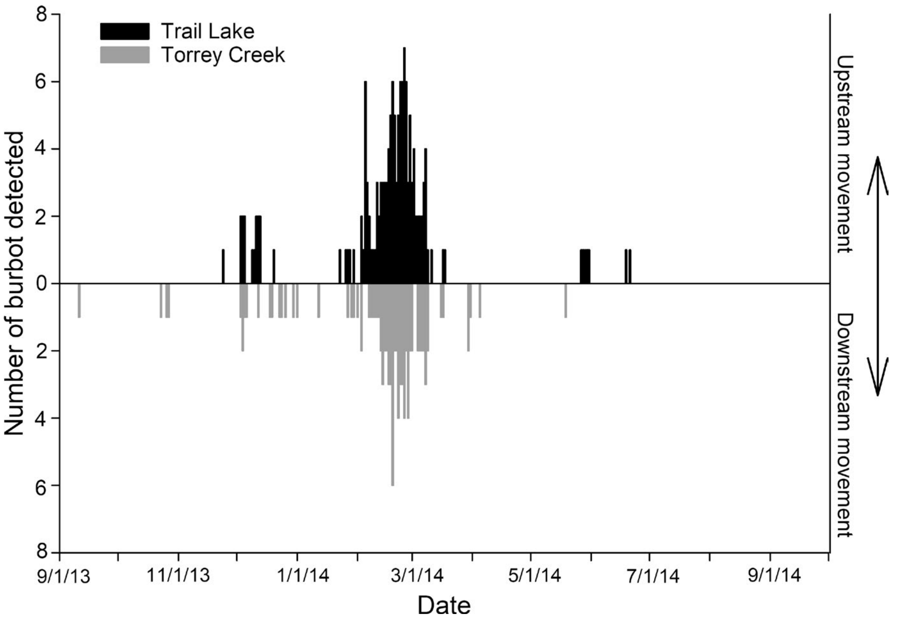

FIGURE 5 Number of unique Trail Lake-origin burbot (black) and Torrey Creek-origin burbot (grey) detected per day at the Torrey Creek PIT antenna array, Wyoming, September 2013–October 2014

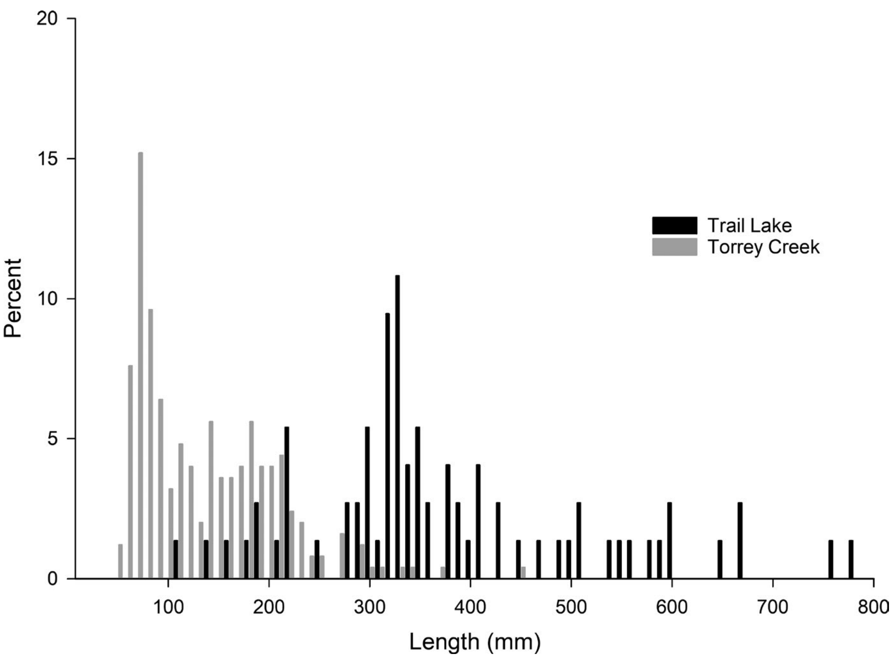

FIGURE 6 Length frequency of burbot sampled in Torrey Creek ($N = 250$) and Trail Lake ($N = 74$), June 2013–October 2014

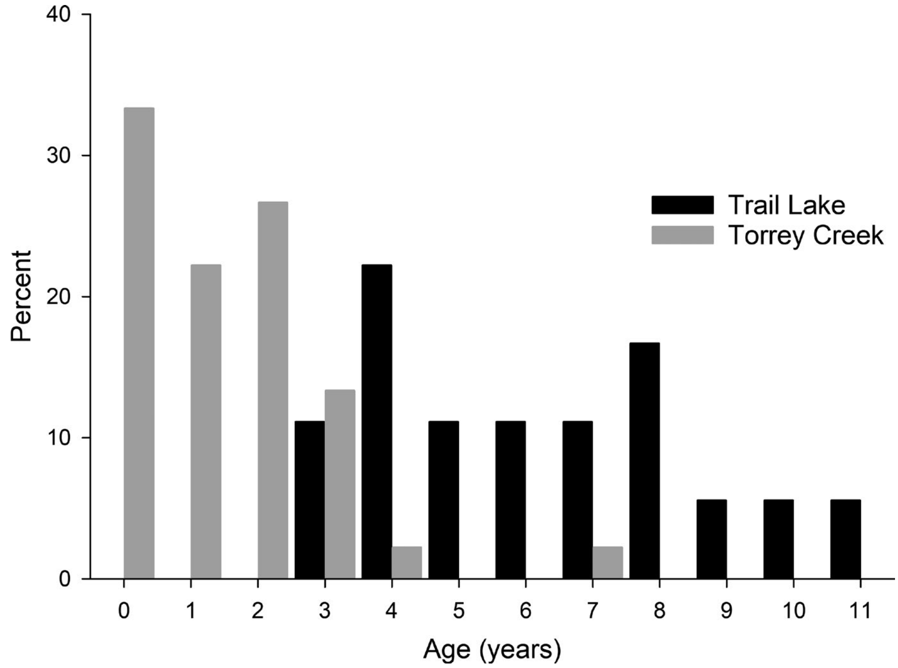

FIGURE 7 Age frequency (in years) of burbot sampled in Torrey Creek ($N = 41$) and Trail Lake ($N = 18$), October 2014

TABLE 1 Mean length ±95% CI (n) with minimum and maximum values of mature and immature burbot ≥ age-1 sampled in Torrey Creek ($N = 26$) and Trail Lake ($N = 18$), October 2014

	Torrey Creek		Trail Lake	
Group	Mean length	Min–Max	Mean length	Min–Max
Mature female	261 ± 101 (6)	196–453	500 ± 102 (8)	368–650
Mature male	167 ± 16 (13)	131–223	444 ± 1,950 (2)	290–597
Immature female	137 ± 53 (3)	124–162	377 ± 60 (7)	323–500
Immature male	150 ± 31 (4)	126–170	345 (1)	–

Note: Length units are in millimeters.

these contiguous lentic and lotic habitats supports historical anecdotal evidence that a subset of the burbot population in the Torrey Creek drainage use Torrey Creek above Trail Lake at a time of year that coincides with spawning. Detection data collected at the PIT antenna array between September 2013 and October 2014 suggest that migration between Trail Lake and Torrey Creek occurs primarily from late winter to early spring, with negligible numbers of detections registered during the remaining year. Similar peaks of migratory activity during the prespawn and spawning periods, with largely sedentary or reduced mobility behavior during other seasons, have been documented throughout the range of burbot (Arndt & Hutchinson, 2000; Brauer et al., 2020; Breeser et al., 1988; Paragamian, 2000; Paragamian & Wakkinen, 2008; Sorokin, 1971). Several studies have also documented migrations from large lakes and rivers into tributary creeks during the spawning period (Breeser et al., 1988; Dillen et al., 2008; Jude et al., 2013; Sorokin, 1971). Similar use of tributary creeks for spawning have been documented in burbot that migrate from Kootenay Lake, Canada, to headwater tributaries in northern Idaho (Breeser et al., 1988). Although long pre- and post-spawning migrations occur in some burbot populations, burbot outmigration from the Torrey Creek drainage into the Wind River is low (Underwood, 2015). Additionally, genetic analysis of burbot in the Wind River drainage revealed that anthropogenic and natural barriers to migratory interchange have resulted in genetic differentiation between the major tributary drainages to the Wind River (Underwood et al., 2016). That said, there is homogenous genetic structure among Torrey, Ring, and Trail lakes within the Torrey Creek drainage, suggesting gene flow occurs within the drainage (Underwood et al., 2016).

Sixty-five percent of PIT-tagged lake-origin fish were not detected. Tagging-caused mortality and tag loss likely did not influence detection rates, as burbot survival (98%) and tag retention (100%) were high after a 365-day period using tagging methods similar to those presented here (Ashton et al., 2014). It is possible that lake-origin burbot were not detected in our study because: (a) tagged burbot spawned in Trail Lake, (b) tagged burbot moved upstream to spawn but stayed in the 1.6 km of Torrey Creek downstream of the PIT antenna array, (c) tagged burbot moved downstream within the Torrey Creek drainage to spawn, or (d) tagged burbot moved past the PIT antenna array undetected. Additionally, we could not confirm if Torrey Creek-origin burbot that were detected migrating downstream entered Trail Lake or remained in Torrey Creek because we were unable to install the antennas at the Torrey Creek confluence. It is possible that the PIT-tagged burbot that moved downstream from the

TABLE 2 Mean age ±95% CI (n) with minimum and maximum values of mature and immature burbot ≥ age-1 sampled in Torrey Creek (N = 26) and Trail Lake (N = 18), October 2014

Group	Torrey Creek Mean age	Torrey Creek Min–Max	Trail Lake Mean age	Trail Lake Min–Max
Mature female	3.8 ± 1.7 (6)	3–7	7.8 ± 1.5 (8)	5–11
Mature male	1.8 ± 0.4 (13)	1–3	6.5 ± 44 (2)	3–10
Immature female	1.7 ± 1.4 (3)	1–2	4.7 ± 1.3 (7)	3–7
Immature male	1.5 ± 0.9 (4)	1–2	4 (1)	–

Torrey Creek antenna array: (a) moved downstream in response to the influx of adult migrants and the increased risk of intraspecific competition, (b) moved downstream of the PIT antenna array to spawn in the lower 1.6 km of Torrey Creek, or (c) moved into Trail Lake to spawn. Although monitoring was nearly continuous throughout the study period, isolated power disruptions in winter 2014 and a damaged PIT reader and dislodged antenna in early summer 2014 resulted in brief gaps in detection coverage. Reader downtime during the summer likely did not influence results of this study because gaps in detection coverage occurred when burbot activity was minimal. However, gaps in detection coverage during the winter may have caused an underestimation of burbot activity during the migratory period.

Differences in length and age structure were observed between Torrey Creek- and Trail Lake-origin burbot. More specifically, Torrey Creek-origin burbot had a smaller size-structure and younger age-structure than Trail Lake-origin burbot. A malfunctioning electrofishing boat prevented shoreline sampling that may have captured younger burbot in Trail Lake in October 2014, but size structure data from the entire study period show that low numbers of small (and likely < age 3) burbot exist in Trail Lake. It is possible that differences in burbot sample sizes and age and length frequencies between lentic and lotic habitats are attributable to sampling gear bias. Trammel nets and cod traps may have skewed size and age structure data towards larger and older fish in Trail Lake. However, monthly night electrofishing in shallow shoreline habitat of Trail Lake also produced low catch rates of small, young burbot during four sampling events from June to September 2013. Additionally, electrofishing gear was effective at capturing burbot of all sizes in the lotic portion of the study area because Torrey Creek is a shallow, clear stream with base flows that are generally <0.28 cubic m/s (unpubl. data). Thus, larger burbot and higher numbers of burbot would have been captured if present during Torrey Creek sampling. Low numbers of burbot captured in Trail Lake by Lewandoski (2015) also corroborate the low sample sizes in this study and suggest burbot exist at a low density in the study area. The substantial proportion of small burbot in Torrey Creek is at least partially explained by the provision of adequate nursery habitat for burbot that hatch there as well as the presence of resident fish that display sexual maturity at a small size. Comparably, tributary creeks in the Big Hole River drainage of Montana may also act as nursery habitat for burbot (Jones-Wuellner & Guy, 2004).

Variable ages at first maturity have been reported throughout the range of burbot. Males as young as age 4 and females as young as age 6 were classified as mature, but males as old as age 14 and females as old as age 16 were classified as immature in the Tanana River, Alaska (Evenson, 1990a). Notably, mature males as young as age 1 and varying in length from 131 to 160 mm occurred in Torrey Creek during this study, and are the youngest and smallest mature burbot reported in Wyoming. Mature male burbot as young as age 1 were also observed in Lake Superior (Bailey, 1972). In contrast to native burbot in the Torrey Creek drainage, lentic burbot matured earlier than lotic burbot outside of their native range in the Green River drainage in Wyoming (Brauer et al., 2019; Klein et al., 2016). More specifically, female burbot in the Green River drainage first matured at age 2 in lentic habitat and age 3 in lotic habitat, while those in the Torrey Creek drainage first matured at age 5 in lentic habitat and age 3 in lotic habitat (Table 2; Brauer et al., 2019; Klein et al., 2016). Additionally, the oldest immature female burbot were age 5 in lentic habitat and age 7 in lotic habitat in the Green River drainage, and age 7 in lentic habitat and age 2 in lotic habitat in the Torrey Creek drainage (Table 2; Brauer et al., 2019; Klein et al., 2016). Differences in burbot age at maturity within and among systems may have been influenced by abiotic (e.g., water temperature) or biotic (e.g., food availability, inherited life-history trait) factors.

Differences in age-at-maturity between Torrey Creek and Trail Lake may be partially explained by Torrey Creek-origin burbot migrating downstream to reside in Trail Lake after reaching maturity. This is supported by the low number of fish sampled in Torrey Creek that were older than age 3. Furthermore, the dearth of burbot age 3 or younger that were sampled in Trail Lake is consistent with the hypothesis that burbot rear in lotic habitat of Torrey Creek before entering the lentic system. It is noteworthy that, despite the described differences in size structure and age structure, Torrey Creek and Trail Lake were found to have similar proportions of mature adults. The sampling of sexually immature burbot from age 4 to age 7 in Trail Lake and sexually mature burbot age 3 and younger in Torrey Creek indicates that at least a subset of Torrey Creek burbot may mature earlier than Trail Lake burbot. Alternative explanations for older, immature burbot occurring in Trail Lake include the sampling of fish that skip spawning between years or the anomalous capture of a sterile burbot (Chen, 1969; Evenson, 1990a; Hewson, 1955; Pulliainen & Korhonen, 1993). The results presented here for Torrey Creek and Trail Lake burbot indicate that resident fluvial and adfluvial life history traits exist within the upper Torrey Creek drainage. Lacustrine-resident burbot that spawn in Trail Lake may also exist, as lacustrine spawning has been documented within the drainage in Ring Lake (Miller, 1970b). However, the results of this study did not definitively answer that question.

Throughout their range, burbot express fluvial, adfluvial, and lacustrine life histories (Brauer et al., 2020; Evenson, 1989, 1990b, 1993; Jude et al., 2013; McPhail & Paragamian, 2000; Sorokin, 1971). Additionally, burbot can adapt to various habitats despite parental origin, as progeny from lacustrine-origin burbot survived, grew, dispersed, and spawned in the Kootenai River (Hardy et al., 2015). The life-history expression of burbot may be highly variable within and among populations and may include cohabitating forms (McPhail & Paragamian, 2000). Similarly, our results indicate that burbot display plasticity in life-history traits in the Torrey Creek drainage. The natural recruitment strategies observed in this study highlight the importance of tributary habitat to burbot in the Torrey Creek drainage. We conclude that Torrey Creek is used by migratory burbot during the spawning period while also supporting a small resident population of burbot that reach sexual maturity earlier than burbot in Trail Lake. Furthermore, given documented interchange between lentic and lotic burbot, it is likely that Torrey Creek provides important nursery habitat for the population. It is still unknown if lacustrine spawning occurs in Trail Lake, and more research is necessary to answer that question. However, preservation of Torrey Creek upstream from Trail Lake should be a priority to conserve fluvial and adfluvial burbot within the Torrey Creek population. The results of this study do confirm that burbot can have varying life-history traits within a small drainage, which may be used to inform habitat conservation and management decisions.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Ahrens, R., & Korman, J. (2002). *What happened to the West Arm Burbot stock in Kootenay Lake? Use of an age-structured population model to determine the possible causes for recruitment failure*. British Columbia Ministry of Water, Land, and Air Protection.

Arndt, S. K., & Hutchinson, J. (2000). Characteristics of burbot spawning in a tributary of Columbia Lake, British Columbia, over a four-year period. In V. L. Paragamian & D. W. Willis (Eds.), *Burbot biology, ecology, and management* (pp. 48–60). American Fisheries Society, Fisheries Management Section.

Ashton, N. K., Anders, P. J., Young, S. P., & Cain, K. D. (2014). Coded wire tag and passive integrated transponder tag implantations in juvenile burbot. *North American Journal of Fisheries Management*, *34*, 391–400. https://doi.org/10.1080/02755947.2014.882458

Bailey, M. M. (1972). Age, growth, reproduction, and food of the burbot, *Lota lota* (Linnaeus), in Southwestern Lake Superior. *Transactions of the American Fisheries Society*, *101*, 667–674. https://doi.org/10.1577/1548-8659(1972)101<667:AGRAFO>2.0.CO;2

Bernard, D. R., Parker, J. F., & Lafferty, R. (1993). Stock assessment of burbot populations in small and moderate-size lakes. *North American Journal of Fisheries Management*, *13*, 657–675. https://doi.org/10.1577/1548-8675(1993)013<0657:SAOBPI>2.3.CO;2

Bjorn, E. E. (1940). Preliminary observations and experimental study of the ling, *Lota maculosa* (LeSueur), in Wyoming. *Transactions of the American Fisheries Society*, *69*, 192–196. https://doi.org/10.1577/1548-8659(1939)69[192:POAESO]2.0.CO;2

Bond, M. H., Hanson, C. V., Baertsch, R., Hayes, S. A., & MacFarlane, R. B. (2007). A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. *Transactions of the American Fisheries Society*, *136*, 562–566. https://doi.org/10.1577/T06-084.1

Brauer, T. A., Quist, M. C., Rhea, D. T., Laughlin, T. W., & Walrath, J. D. (2019). Population characteristics and management of lentic populations of nonnative burbot in the Green River system, Wyoming. *North American Journal of Fisheries Management*, *39*, 45–57. https://doi.org/10.1002/nafm.10247

Brauer, T. A., Quist, M. C., Rhea, D. T., Laughlin, T. W., & Waring, E. (2020). Movement dynamics of nonnative burbot in the upper Green River system and implications for management. *North American Journal of Fisheries Management*, *40*, 1161–1173. https://doi.org/10.1002/nafm.10480

Breeser, S. W., Stearns, F. D., Smith, M. W., West, R. L., & Reynolds, J. B. (1988). Observations of movements and habitat preferences of burbot in an Alaskan glacial river system. *Transactions of the American Fisheries Society*, *117*, 506–509. https://doi.org/10.1577/1548-8659(1988)117<0506:OOMAHP>2.3.CO;2

Chen, L. C. (1969) The biology and taxonomy of the burbot, *Lota lota leptura*, in interior Alaska. Biological Papers of the University of Alaska 11.

Connolly, P. J., Jezorek, I. G., Martens, K. D., & Prentice, E. F. (2008). Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. *North American Journal of Fisheries Management*, *28*, 402–417. https://doi.org/10.1577/M07-008.1

Cott, P., Johnston, T., & Gunn, J. (2011). Food web position of burbot relative to lake trout, northern pike, and lake whitefish in four sub-Arctic boreal lakes. *Journal of Applied Ichthyology*, *27*, 49–56. https://doi.org/10.1111/j.1439-0426.2011.01843.x

Dillen, A., Coeck, J., & Monnier, D. (2008). Habitat use and seasonal migrations of burbot in lowland rivers in north France. In V. L. Paragamian & D. H. Bennett (Eds.), *Burbot: Ecology, management, and culture* (pp. 29–42). Symposium 59 of the American Fisheries Society.

Evenson, M. J. (1989) Biological characteristics of burbot in rivers of interior Alaska during 1988. Fishery Data Series No. 109 Alaska Department of Fish and Game, Division of Sport Fish, Anchorage, AK.

Evenson, M. J. (1990a). Age and length at sexual maturity of burbot in the Tanana River, Alaska. Fish manuscript no 90-2, Alaska Department of Fish and Game, Division of Sport Fish, Anchorage, AK.

Evenson, M. J. (1990b) Movement, abundance, and length composition of burbot in rivers of interior Alaska during 1989. Fishery Data Series 90-3, Alaska Department of Fish and Game, Division of Sport Fish, Anchorage, AK.

Evenson, M. J. (1993) Seasonal movements of radio-implanted burbot in the Tanana River drainage. Alaska Department of Fish and Game, Fishery Data Series No. 93-47, Anchorage, AK.

Greenberg, L. A., & Giller, P. S. (2000). The potential of flat-bed passive integrated transponder antennae for studying habitat use by stream fishes. *Ecology of Freshwater Fish*, *9*, 74–80. https://doi.org/10.1034/j.1600-0633.2000.90108.x

Hagan, G. O. (1952). Ling Hatching Experiment, Cokeville, Wyoming. Wyoming Game Fish Commission Administrative Report, Fish Division, Cheyenne.

Hardy, R. S., & Paragamian, V. L. (2013). A synthesis of Kootenai River burbot stock history and future management goals. *Transactions of the American Fisheries Society*, *142*, 1662–1670. https://doi.org/10.1080/00028487.2013.790845

Hardy, R. S., Stephenson, S. M., Neufeld, M. D., & Young, S. P. (2015). Adaptation of lake-origin burbot stocked into a large river environment. *Hydrobiolgia*, *757*, 35–47. https://doi.org/10.1007/s10750-015-2226-0

Hewson, L. C. (1955). Age, maturity, spawning and food of burbot, *Lota lota*, in Lake Winnipeg. *Journal of the Fisheries Research Board of Canada*, *12*, 930–940.

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

Hooley-Underwood, Z., Mandeville, E. G., Gerrity, P., Deromedi, J., Johnson, K., & Walters, A. W. (2018). Combining genetic, isotopic, and field data to better describe the influence of dams and diversions on burbot movement in the Wind River drainage, Wyoming. *Transactions of the American Fisheries Society*, *147*, 606–620. https://doi.org/10.1002/tafs.10062

Hubert, W. A., Dufek, D., Deromedi, J., Johnson, K., Roth, S., & Skates, D. (2008). Burbot in the Wind River drainage of Wyoming: Knowledge of stocks and management. In V. L. Paragamian & D. H. Bennett (Eds.), *Burbot: Ecology, management, and culture* (pp. 187–199). Symposium 59 of the American Fisheries Society.

Jacobs, G. R., Madenjian, C. P., Bunnell, D. B., & Holuszko, J. D. (2010). Diet of lake trout and burbot in Northern Lake Michigan during spring: Evidence of ecological interaction. *Journal of Great Lakes Research*, *36*, 312–317. https://doi.org/10.1016/j.jglr.2010.02.007

Jones-Wuellner, M. R., & Guy, C. S. (2004). *Status of burbot in Montana*. Montana Cooperative Fishery Research Unit.

Jude, D. J., Wang, Y., Hensler, S. R., & Janssen, J. (2013). Burbot early life history strategies in the Great Lakes. *Transactions of the American Fisheries Society*, *142*, 1733–1745. https://doi.org/10.1080/00028487.2013.795192

Klein, Z. B., Quist, M. C., Rhea, D. T., & Senecal, A. C. (2016). Population characteristics and the suppression of nonnative burbot. *North American Journal of Fisheries Management*, *36*, 1006–1017. https://doi.org/10.1080/02755947.2016.1173137

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

Lewandoski, S. A. (2015). Exploitation of burbot *Lota lota* in the Wind River drainage, Wyoming. Master's thesis, Montana State University.

Lewandoski, S. A., Guy, C. S., Zale, A. V., Gerrity, P. C., Deromedi, J. W., Johnson, K. M., & Skates, D. L. (2017). Empirical estimation of recreational exploitation of burbot, *Lota lota*, in the Wind River drainage of Wyoming using a multistate capture-recapture model. *Fisheries Management and Ecology*, *24*, 298–307.

McBaine, K. E., Klein, Z. B., Quist, M. C., & Rhea, D. T. (2018). Diet of burbot and implications for sampling. *Intermountain Journal of Sciences*, *24*, 1–13.

McPhail, J. D., & Paragamian, V. L. (2000). Burbot biology and life history. In V. L. Paragamian & D. W. Willis (Eds.), *Burbot biology, ecology, and management* (pp. 11–23). American Fisheries Society, Fisheries Management Section.

Miller, D. D. (1970a). A life history study of the burbot in Ocean Lake and Torrey Creek, Wyoming. Master's thesis, University of Wyoming.

Miller, D. D. (1970b). A life history study of burbot in Boysen Reservoir, Ring Lake, and Trail Lake. Wyoming Game and Fish Commission, Project number F-41-R-2. Lander, Wyoming.

Paragamian, V. L. (2000). The effects of variable discharges on burbot spawning migrations in the Kootenai River, Idaho, USA, and British Columbia, Canada. In V. L. Paragamian & D. W. Willis (Eds.), *Burbot biology, ecology, and management* (pp. 111–123). American Fisheries Society, Fisheries Management Section.

Paragamian, V. L., & Wakkinen, V. D. (2008) Seasonal movement of burbot in relation to temperature and discharge in the Kootenai River, Idaho, USA and British Columbia, Canada. In V. L. Paragamian & D. H. Bennett (Eds.), *Burbot: Ecology, management, and culture* (pp. 55–77). Symposium 59 of the American Fisheries Society.

Paragamian, V. L., Whitman, V., Hammond, J., & Andrusak, H. (2000). Collapse of burbot fisheries in the Kootenai River, Idaho, USA, and Kootenay Lake, British Columbia, Canada. In V. L. Paragamian & D. W. Willis (Eds.), *Burbot biology, ecology, and management* (pp. 155–164). American Fisheries Society, Fisheries Management Section.

Pulliainen, E., & Korhonen, K. (1993). Does the burbot, *Lota lota*, have rest years between normal spawning seasons. *Journal of Fish Biology*, *43*, 355–362.

Quinn, S. (2000). The status of recreational fisheries for burbot in the United States. In V. L. Paragamian & D. W. Willis (Eds.), *Burbot biology, ecology, and management* (pp. 127–135). American Fisheries Society, Fisheries Management Section.

Sorokin, V. N. (1971). The spawning and spawning grounds of the burbot, *Lota lota* (L.). *Journal of Ichthyology*, *11*, 907–916.

Stapanian, M. A., Paragamian, V. L., Madenjian, C. P., Jackson, J. R., Lappalainen, J., Evenson, M. J., & Neufeld, M. D. (2010). Worldwide status of burbot and conservation measures. *Fish and Fisheries*, *11*, 34–56. https://doi.org/10.1111/j.1467-2979.2009.00340.x

Stuby, L. (2008) An evaluation of precision in age assessment of thin-sectioned and whole otoliths and the efficacy of using oxytetracycline as an aid in validating otolith annuli in burbot. In: V. L. Paragamian & D. H. Bennett (Eds.), *Burbot: Ecology, management, and culture* (pp. 235–247). Symposium 59 American Fisheries Society.

Underwood, Z. E. (2015). The movements and population structure of burbot (*Lota lota*) in the Wind River, Wyoming. Master's thesis, University of Wyoming.

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

Williams, F. (1959). Progress report on life history investigations of the burbot. Wyoming Game and Fish Commission, Project number 2355-2-2, Cheyenne.

Wyoming Game and Fish Department, 2017Wyoming Game and Fish Department. (2017). State Wildlife Action Plan 2017. Wyoming Game and Fish Department, Cheyenne.

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