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ARTICLE

Temporal Variation in Capture Efficiency Underrepresents Spring Out-Migrating Bull Trout in a Trap-and-Haul Program

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Abstract
Trap-and-haul programs can maintain connection among habitats for migratory salmonids in fragmented systems. To conserve diversity within and among life history strategies, downstream trap and transport of juvenile salmonids could ideally mimic the natural, underlying out-migration dynamics of the population. A two-way trap-and-haul program is implemented in the lower Clark Fork River, Montana, to conserve adfluvial Bull Trout *Salvelinus confluentus*. We used PIT technology to assess whether downstream trapping efforts are effectively capturing variation in the out-migration dynamics of juvenile Bull Trout in Graves Creek, a key spawning and rearing tributary in the system. We tagged 821 juvenile Bull Trout in Graves Creek and used these tagged Bull Trout in conjunction with stationary PIT antennas to monitor out-migration and evaluate efficiency of the downstream trapping program. Capture efficiency in Graves Creek varied substantially from autumn to spring, with 89–96% of autumn out-migrating Bull Trout captured and 5–10% of spring out-migrating Bull Trout captured. Overall, we found that Bull Trout transported during the autumn out-migration periods generally reflect the natural out-migration dynamics of the population; however, Bull Trout that out-migrate in the spring are currently underrepresented in the downstream transport program. By understanding the underlying out-migration dynamics of the Bull Trout population in Graves Creek, management of the downstream trapping efforts can focus on minimizing potential selection for or against out-migrants based on timing and age at out-migration. Minimizing selection will conserve variation within the adfluvial life history strategy and therefore maximize resilience of the adfluvial Bull Trout populations.

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As anthropogenic threats to the biodiversity of freshwater fish species increase, there is a pressing need to focus conservation efforts on actions that will increase the resilience of populations (Waldman et al. 2016). In this context, resilience is defined as the ability of a population to persist in the face of disturbance or change (Holling 1973). Many species of salmonids express diverse life history strategies, which are thought to be an evolutionary adaptation that allows species to persist in variable environments (Schindler et al. 2010; Tamario et al. 2019). Conserving migratory life history strategies in salmonid populations can be challenging due to widespread habitat fragmentation from physical and thermal barriers. In some cases, the migratory life history component of salmonid populations may be restored by the removal of a barrier such as a dam, allowing habitats to reconnect (Quinn et al. 2017; Brenkman et al. 2019). However, barrier removal is often not an option; therefore, there is an increasing need for solutions to restore and maintain migratory life history strategies in systems that remain fragmented by barriers. One solution is the implementation of a trap-and-haul program, where fish are physically moved upstream or downstream of a barrier. Trap-and-haul programs have been employed for a variety of species, including anadromous salmonids (Kock et al. 2018; Naughton et al. 2018), lamprey (family Petromyzontidae) (Corbett et al. 2014), and small-bodied fish species (Harris et al. 2019).

Trap-and-haul programs can enable connectivity in populations when physical characteristics of a dam and associated habitat, or characteristics of the species, render passive efforts such as fish ladders ineffective (Bunt et al. 2012; Silva et al. 2018; Harris et al. 2019). However, trap-and-haul programs are resource intensive and the high degree of human intervention that is involved may have unintended consequences. The extent of these consequences, such as altering behavior, influencing migration timing, and unintentionally imposing selective pressure, may be difficult to fully understand and quantify (Budy et al. 2002; Muir et al. 2006; Al-Chokhachy et al. 2015). Multiple aspects of trap-and-haul programs may impose selective pressures, such as size selectivity of the gear used to capture fish for transport or selection on timing of out-migration because of the timing and duration of trapping seasons. To effectively manage trap-and-haul programs for maximum benefit to the population, it is fundamental to understand the underlying out-migration dynamics of the population and how capture methods may influence these dynamics. Without this understanding, natural resource agencies may inadvertently reduce the life history variation present in populations by imposing selective pressures, ultimately reducing the resilience of the population rather than increasing it (Schindler et al. 2010; Kock et al. 2020).

In the early 2000s, a two-way trap-and-haul program was implemented to reestablish connectivity between local Bull Trout *Salvelinus confluentus* populations (i.e., a population of Bull Trout that spawn within the same tributary) in the lower Clark Fork River and Lake Pend Oreille, restoring the historic adfluvial migratory life history component of the lower Clark Fork River population (Neraas and Spruell 2001; Epifanio et al. 2003; DeHaan et al. 2011). In this program, adult Bull Trout are captured at the base of Cabinet Gorge Dam and transported upstream to their most likely region of origin, determined by PIT tag for previously tagged fish or rapid-response genetic identification for untagged fish, to allow access to their natal streams to spawn (DeHaan et al. 2011). The juvenile Bull Trout trap-and-haul program (hereafter, "downstream program") was implemented to address concerns that passage through the reservoirs caused a high amount of mortality in out-migrating juveniles due to seasonally warm water temperatures and the presence of nonnative piscivorous species (USFWS 2015b). In the downstream program, juvenile Bull Trout are captured within their natal streams as they begin to out-migrate and are transported directly to Lake Pend Oreille. Juvenile Bull Trout that are not captured by the traps enter the reservoir system and either migrate volitionally downstream to Lake Pend Oreille or use the reservoir system as a surrogate for the lake habitat (hereafter, "reservoir-type").

The Bull Trout two-way trap-and-haul program has been successful in restoring the adfluvial life history strategy of Bull Trout that use Lake Pend Oreille for growth to maturity as evidenced by successful returns of juvenile transports as spawning adults to natal streams (DeHaan and Bernall 2013). Thus far, the number of juvenile out-migrants captured in springtime traps has served as the primary source of information driving management decisions. Using the number of Bull Trout captured in the traps as a metric of success without explicitly quantifying and accounting for capture efficiency has led to a limited and potentially biased knowledge base regarding the underlying out-migration dynamics of these populations. Therefore, it is unknown whether the downstream trapping program is effectively capturing variation in the age and timing of out-migration or whether the trapping program is imposing selection.

Typical mark–recapture methods for quantifying capture efficiency involve taking a subset of fish that are captured in the trap daily (or at another predetermined time interval) and rereleasing those fish upstream of the trap (Volkhardt et al. 2007). The number that are subsequently recaptured in the trap are then used to determine efficiency (Volkhardt et al. 2007). There are drawbacks to using this method in the context of a trap-and-haul program, particularly for species with variable out-migration dynamics, such as juvenile Bull Trout. The seasonal timing of out-migration for juvenile Bull Trout, and the age at which juvenile Bull Trout out-migrate, can vary substantially within and among systems (Rieman and McIntyre 1993; Al-Chokhachy and Budy 2008; Howell et al. 2016). Therefore, it is difficult to determine when to implement trapping efforts to capture juvenile Bull Trout unless traps are operated year-round for multiple years under varying conditions, which is resource intensive. Additionally, the mark–recapture assumption that fish captured in the trap do not vary from those not captured may be violated when multiple age-classes of fish are out-migrating and size selectivity of the trap is unknown.

There are additional concerns associated with using the mark–recapture method for fish in a trap-and-haul program as releasing fish upstream of the trap means risking the loss of potential transports if the fish are not recaptured. This may be particularly problematic for threatened or endangered species or for species that face certain mortality if not transported. Finally, if there is variability in season-specific capture probability to the point where capture probability approaches zero under certain conditions, there is a possibility that capture probability could not be estimated for the period of time under those conditions because zero or very few fish would be captured to begin with.

Passive integrated transponder tags and stationary PIT antennas have been widely used to better understand multiple aspects of fish behavior in streams, such as movement and out-migration (Horton et al. 2007) and habitat use (Greenberg and Giller 2000). The PIT antennas enable continuous monitoring of out-migration and use all tagged fish to quantify capture efficiency, eliminating the potential bias associated with calculating capture efficiency using fish that have previously been captured in the trap. Using PIT antennas to monitor out-migration and quantify capture efficiency may reveal out-migration dynamics that were previously masked due to violated assumptions or sampling constraints and biases associated with traditional mark–recapture methods. To address the knowledge gap regarding the effectiveness of the current downstream transport program, substantial investments into infrastructure have been made to facilitate applied research in Graves Creek, one of the primary streams in the downstream trap-and-haul program. The infrastructure includes the construction of multiple stationary, permanent PIT antennas positioned near the permanent weir trap used to collect out-migrants from Graves Creek.

We used the stationary PIT antennas to develop a better understanding of the underlying out-migration dynamics of juvenile adfluvial Bull Trout in Graves Creek and to assess how the current downstream trapping program may be influencing these dynamics. We sought to answer the following questions: (1) what is the current capture efficiency of the downstream trap; (2) what is the total number of out-migrating Bull Trout from Graves Creek by age, adjusted for capture efficiency of the traps; (3) what is the distribution of out-migration events annually; and (4) do the downstream trapping methods effectively capture variation in age and timing of out-migrating Bull Trout? Understanding the underlying out-migration dynamics of the populations will enable the identification of potential sources of selection within the downstream trapping program. Identifying potential sources of selection will inform management to ensure the downstream program continues to conserve the full range of adfluvial life history dynamics, thus increasing the resiliency of the populations.

STUDY SITE

The Clark Fork River originates near Butte, Montana, and flows in a northwest direction for nearly 500 km before reaching Lake Pend Oreille, Idaho. Historically, the lower Clark Fork River served as a migration corridor for adfluvial Bull Trout, which would spawn and rear in Montana tributaries before migrating downstream to Lake Pend Oreille for growth to maturity (Pratt 1985). From 1913 to 1959, three hydropower dams were constructed on the lower Clark Fork River with no fish passage facilities (Figure 1). The dams isolated at least 15 local Bull Trout populations that likely were previously migratory to Lake Pend Oreille (Pratt and Huston 1993; USFWS 2015a). The downstream-most dam, Cabinet Gorge Dam, is located in Idaho approximately 16 km upstream from confluence of the Clark Fork River with Lake Pend Oreille (Figure 1). Cabinet Gorge Reservoir spans approximately 32 km upstream to Noxon Rapids Dam (Figure 1). Noxon Reservoir spans 60 km upstream from Noxon Rapids Dam to Thompson Falls Dam (Figure 1).

Graves Creek enters the north side of Noxon Reservoir (Figure 1) as a fourth-order stream, with a length of approximately 21 km. Graves Creek Falls is a natural barrier to upstream fish passage located at river kilometer 5.2 on Graves Creek (measuring from its confluence with the Clark Fork River), and Bull Trout distribution is limited to the reach downstream of the falls, where this study occurred. Despite the small area of habitat inhabited by Bull Trout, Graves Creek has consistently contributed a large proportion of out-migrants to the downstream transport program (DeHaan and Bernall 2013). Bull Trout and Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* are the most predominant species present downstream of Graves Creek Falls. From 2002 through 2012, juvenile Bull Trout in Graves Creek were captured for the trap-and-haul program using screw traps and temporary weir traps. In 2012, a permanent, concrete-bedded weir trap was constructed in Graves Creek, and operation of the permanent weir began in 2013. A permanent PIT-

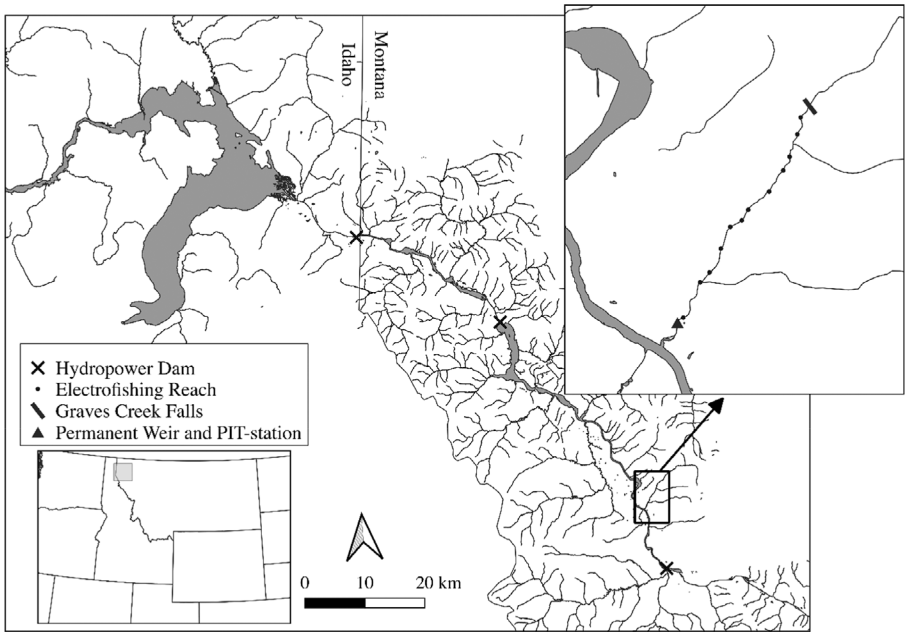

FIGURE 1. Lower Clark Fork River watershed in western Montana. Upper right inset map depicts the study area on Graves Creek, showing the locations of the sampling reaches. The lower left inset map depicts the location of the study in the states of Idaho and Montana. Maps were created using QGIS 3.4.7, with layers from the U.S. Geological Survey National Hydrography Dataset.

monitoring station is also present, with two antennas located 2 and 12 m upstream of the weir, two integrated into the weir, and two antennas 2 and 20 m downstream of the weir (Figure 2).

METHODS

Tagging methods.— During the summers of 2019 and 2020, juvenile Bull Trout were sampled at twelve 100-m reaches in Graves Creek (Figure 1). Reaches were selected using a stratified random sampling design. A backpack electrofisher (Smith-Root; LR-24 model) was used in a downstream direction to a block net. All fish that were sampled were measured for total length (mm) and weight (g) and scanned for the presence of a PIT tag. If a PIT tag was not detected, Bull Trout >100 mm received a 12-mm full duplex PIT tag. Prior to tag insertion, Bull Trout were anesthetized with Aqui-S. A disinfected needle or Biomark MK25 injector was used to insert the PIT tag into the anterior dorsal sinus. Bull Trout were returned to live cars and, once recovered, were released throughout the sampling reach. We did not attempt to capture or enumerate age-0 Bull Trout because they were not fully recruited to the gear and would not meet the minimum

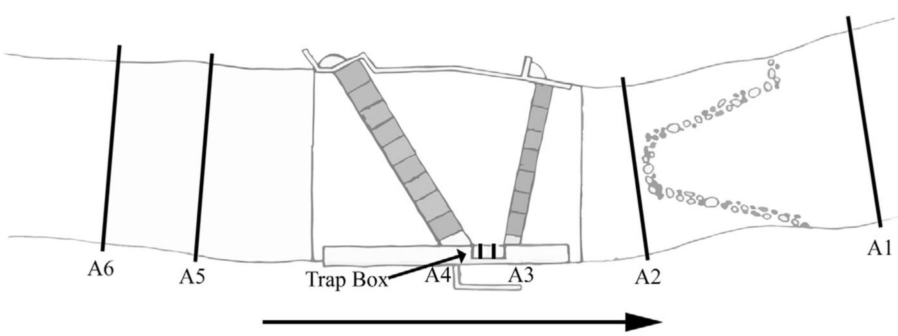

FIGURE 2. Diagram of the permanent weir and stationary PIT antennas located at river kilometer 0.5 on Graves Creek, with the arrow indicating direction of flow. The permanent weir trap was comprised of two rows of weir panels attached to a concrete slab. Antennas are depicted with an “A” preceding the number; A6 and A5 are located upstream of the trap, A4 and A3 are located within the trap box, and A2 and A1 are located downstream of the trap.

size requirement for PIT tagging. We tagged 821 juvenile Bull Trout in Graves Creek.

Trapping operations.— Out-migrating Bull Trout were captured using the permanent, concrete-bedded weir trap located at river kilometer 0.5 (Figures 1 and 2). The permanent weir trap was comprised of two rows of weir panels attached to a concrete slab. The upstream row was comprised of nine panels with 13-mm-diameter vertical pickets on each panel and a 13-mm space between panels. The downstream row was comprised of seven panels with 13-mm-diameter vertical pickets on each panel and a 19-mm space between panels of vertical pickets. The upstream row guided downstream-moving fish to a recessed channel in the concrete that terminated at the entrance to a 254-mm pipe. Fish traveled down the pipe that terminated with a short (~254 mm) outfall into a trap box. The downstream weir guided upstream-moving fish to the same recessed channel that terminated at the entrance to a trap box. The permanent weir trap was operated in the autumn of 2019 (September 4 to November 27, 2019), spring of 2020 (April 15 to July 2, 2020), autumn of 2020 (September 2 to November 20, 2020), and spring of 2021 (March 29 to July 2, 2021). The weir trap was checked daily for fish and cleared of debris. During the autumn trapping seasons, panels were lowered on the trap once per week from the start of trapping through October 6 to allow for volitional passage of adult Bull Trout, which left the trap partially fishing. During the spring 2020 trapping season, all panels were lowered and the trap box was removed each weekend due to logistic limitations.

All fish captured in the traps were measured for total length (mm) and weight (g) and scanned for the presence of a PIT tag. Bull Trout that met the minimum size limit for transport (≥120 mm) were transported 80 km to a release site below Cabinet Gorge Dam. Bull Trout that were under the size limit were released below the traps. Bull Trout <100 mm captured in the trap were not included in the results because they did not meet the minimum size requirement for tagging.

Aging.— Scales were removed from juvenile Bull Trout to estimate age structure during summer sampling. Scales were removed from all sampled Bull Trout above the lateral line ventral to the leading edge of the dorsal fins using a clean knife. In the lab, scales from 10 fish were randomly selected from each 10-mm length-class for aging. Photographs of the scales were acquired using a Leica microscope, and the photographs of scales were aged individually by two readers. Readers did not have knowledge of fish length prior to aging. When age estimates did not agree between readers, scales were aged again, and on rare occasions, a third independent reader was consulted to determine the age. If an agreement could not be reached or the quality was deemed too low to accurately determine an age, the sample was excluded, and an alternate fish was randomly selected from the size-class. The "FSA" package in R (Ogle et al. 2020) was used to construct a length-at-age key. The length-at-age key was then used to assign ages to all Bull Trout sampled, following methods outlined by Isermann and Knight (2005). Year-class was also assigned based on the year that the Bull Trout emerged (e.g., the 2018 year-class was a product of redds in 2017) to enable tracking of cohorts through time. Age structure of out-migrating Bull Trout during the trapping seasons was estimated using Bull Trout that were previously tagged and aged during summer sampling and subsequently captured in the trap. A new length-at-age relationship was constructed based on the length of the Bull Trout when captured in the trap and used to assign ages to all Bull Trout captured in the trap during the autumn trapping seasons. During the spring trapping seasons, a limited number of previously aged Bull Trout captured in the trap prevented the construction of a new length-at-age key. Although we were able to identify age-1 Bull Trout based on their length being below the expected threshold for age-2 fish at this time of year, we were unable to differentiate between age-2 and age-3 fish due to the lack of recaptured tagged out-migrants. Therefore, age at out-migration information for spring out-migrants was limited to fish that were previously aged (i.e., tagged Bull Trout that were trapped or detected out-migrating).

Capture efficiency.— In Graves Creek, we assessed capture efficiency of the permanent weir trap and of the overall seasonal capture efficiency of the downstream trapping program using the stationary PIT antennas and out-migrating Bull Trout that were tagged in summer sampling. During trapping seasons, if a Bull Trout approached the trap and was detected on at least one upstream antenna (A6, A5) and was subsequently captured in the trap, it was considered a capture (Figure 2). If a tagged Bull Trout was detected on at least one downstream antenna (A1, A2) without being captured in the trap, it was considered a missed fish (Figure 2). Missed fish were further grouped into the following categories: fish missed when the trap was partially fishing for volitional passage, fish missed when the trap was not in place for weekends or holidays, fish missed when the trap was in place but known to be compromised (e.g., clogged with debris, overtopped), and fish missed for unknown reasons (i.e., trap appeared to be fully fishing).

Capture efficiency of the weir was calculated as the proportion of captured fish that were previously tagged out of the total number of tagged Bull Trout that out-migrated (i.e., captured fish and missed fish). Capture efficiency was calculated by age-class (when possible) for each season. Calculations for capture efficiency of the weir did not include fish missed during volitional passage days or when the trap was not fishing for weekends or holidays.

Overall capture efficiency was calculated based on fish missed for any reason, including volitional passage or when fish were missed when the trap was not fishing for weekends or holidays.

Total number of out-migrants.— Total number of out-migrants by age-class during each trapping season in Graves Creek was estimated using a Peterson equation with a Chapman modification, which was modified to enable estimation with the PIT antennas (Volkhardt et al. 2007):

$$\widehat{N}_i = \frac{(M_i+1)(n_i+1)}{(m_i+1)} - 1,$$

where during discrete time period i, M_i is the total number of tagged Bull Trout that out-migrated and were either captured in the trap or missed by the trap, n_i is the total number of Bull Trout captured in the trap (including tagged and untagged Bull Trout), and m_i is the total number of tagged Bull Trout that out-migrated and were captured in the trap. Total number of out-migrants was calculated separately for each age-class during autumn trapping seasons and was calculated for age-2 and older fish during spring trapping seasons, with the duration of the trapping season representing the discrete time period i. The calculation for the total number of out-migrating Bull Trout included all fish that were missed for the season, including fish missed on volitional passage days and on weekends and holidays. Variance was calculated using the following equation developed by Seber (1970):

$$V\left(\widehat{N}_i\right) = \frac{(M_i+1)(n_i+1)(M_i-m_i)(n_i-m_i)}{(m_i+1)^2(m_i+2)}.$$

During the autumn 2020 trapping season on Graves Creek, an American mink *Neovison vison* entered the trap box and removed multiple fish. Mink predation was first suspected when multiple tagged fish were detected on A3 as they entered the trap box but subsequently disappeared (Figure 2). The presence of an American mink preying on fish in the trap box was confirmed with a game camera. Of the 85 tagged age-2 Bull Trout that entered the trap box, 33% are believed to have been removed by American mink. The percentage of tagged fish that were removed by American mink was applied to the number of untagged age-2 Bull Trout captured to estimate the total number of Bull Trout that may have been removed by American mink.

Detection probability was calculated for each full span antenna (i.e., A6, A5, A2, A1; Figure 2) using the formula described in Appendix 1 of Conolly et al. (2008). Detection probability was calculated using fish that were not captured in the trap but were detected on one of the downstream antennas to ensure that the fish did make a full pass of the antennas. The probability that a fish would be detected on at least one downstream antenna (A1 or A2) and therefore considered an out-migrant was calculated by season. Detection probability was used to adjust estimates of the number of Bull Trout missed by the trap by season.

Timing of out-migration and overall efficiency of downstream trapping methods.— Out-migration from Graves Creek was monitored using the stationary PIT antennas. The upstream (A6, A5) and downstream (A1, A2) antennas were operated year-round, while A3 and A4 were only operational during the trapping seasons (Figure 2). Bull Trout were considered out-migrants if they were detected on at least one downstream antenna or captured in the trap. Overall efficiency of the current downstream trapping efforts was assessed using the fates assigned above for the trapping seasons, along with fish that out-migrated during seasons when the trap was not fishing. Out-migration of tagged Bull Trout was tracked over the duration of the study (July 2019–July 2021), with data downloaded periodically. Out-migration date was assigned to a fish based on the last date of detection.

RESULTS

Capture Efficiency of Traps

Capture efficiency of the permanent weir varied substantially between autumn and spring trapping seasons (Table 1). During the autumn 2019 trapping season, capture efficiency of the permanent weir in Graves Creek varied by age-class, with the lowest efficiency for age-1 Bull Trout (83%; Table 1). Capture efficiency for age-2 Bull Trout was 95% (Table 1), and capture efficiency was 100% for age-3 Bull Trout (Table 1). Mean capture efficiency of the weir for all age-classes was 93%, and mean overall efficiency was 89% because of three fish out-migrating on volitional passage days (Table 1). The probability of a fish being detected on antenna A1 or A2 was 99%, leading to an adjustment of two fish that may have been missed by the trap and not detected on either of the downstream antennas (see total adjusted in Table 1). In the spring 2020 trapping season, capture efficiency estimation was limited to age-2 and older Bull Trout (age-1 Bull Trout were below the minimum tagging length during summer sampling). Capture efficiency during the spring was substantially lower than the autumn, at 14% for age-2 and older Bull Trout (Table 1). The majority of Bull Trout in the spring were missed when the weir was known to be compromised due to conditions (e.g., high flows necessitating partial removal of the trap) (Table 1). Overall efficiency during the spring was 10%, a result of 20 fish out-migrating during weekends when the trap was not operating (Table 1). Detection probability of the downstream antennas was 94%, leading to an adjustment of 27 fish

TABLE 1. Capture efficiency and number of out-migrating Bull Trout from Graves Creek during the autumn 2019 (September 4 to November 27, 2019), spring 2020 (April 15 to July 2, 2020), autumn 2020 (September 2 to November 20, 2020), and spring 2021 (March 29 to July 2, 2021) trapping seasons. Trapped fish are classified as previously tagged (T) or not tagged (NT), and missed fish are classified based on the reason for being missed: unknown (U), compromised due to conditions (C), weekend or holiday (W), or volitional passage (VP). Capture efficiency of the permanent weir (CE) was calculated using fish missed for unknown reasons or when the trap was partially fishing, whereas overall efficiency (OE) included all fish missed during the trapping season, and the number of out-migrants was estimated based on overall efficiency. The adjusted total number of missed and out-migrating Bull Trout was calculated based on the probability that a tagged fish out-migrated and was not detected on at least one downstream antenna.

	Trapped		Missed							
Age (year-class)	T	NT	U	C	W	VP	CE (%)	OE (%)	Estimated missed (95% CI)	Estimated number of out-migrants (95% CI)
Autumn 2019										
Age 1 (2018)	55	442	11	0	0	1	83	82	107 (62)	604 (62)
Age 2 (2017)	19	183	1	0	0	2	95	86	30 (34)	232 (34)
Age 3 (2016)	1	4	0	0	0	0	100	100	0	5
Mean							93	89		
Total	75	629	12	0	0	3			136 (96)	841 (96)
Total adjusted									138 (98)	843 (98)
Spring 2020										
Age 1 (2019)		2								2
Age 2+ (2017, 2018)	9	41	5	52	20	0	14	10	393 (221)	443 (221)
Mean							14	10		
Total	9	43	5	52	20	0			393 (221)	445 (221)
Total adjusted									420 (248)	472 (248)
Autumn 2020										
Age 1 (2019)	4	71	0	0	0	0	100	100	0	75
Age 2 (2018)	85[a]	451[b]	1	2	3	4	97	89	62 (37)	598 (37)[b]
Age 3 (2017)	1	4	0	0	0	0	100	100	0	5
Mean							99	96		
Total	90[a]	526[b]	1	2	3	4			62 (37)	678 (37)[b]
Total adjusted									63 (38)	679 (38)[b]
Spring 2021										
Age 2+ (2018, 2019)	1	12	5	16	0	0	5	5	147 (82)	160 (82)
Mean							5	5		
Total	1	12	5	16	0	0			147 (82)	160 (82)
Total adjusted									186 (121)	199 (121)

[a]Number includes Bull Trout that were captured in the trap but subsequently removed due to mink predation.
[b]Number includes 149 Bull Trout estimated to have been removed by mink.

that may have been missed by the trap and not detected (see total adjusted in Table 1). Capture efficiency during the autumn 2020 trapping season was high overall, with 100% estimated efficiency for age-1 and age-3 Bull Trout and 97% efficiency for age-2 Bull Trout (Table 1). Mean capture efficiency of the weir for all age-classes was 99%, and overall efficiency was 96% because of four fish out-migrating on volitional passage days and three fish out-migrating on holidays (Table 1). Detection probability of the downstream antennas during autumn 2020 was 98%, leading to an adjustment of one missed fish (see total adjusted in Table 1). Capture efficiency during the spring of 2021 was 5% for age-2 and older Bull Trout, with 16 fish missed when the trap was known to be compromised by conditions, and 5 missed for unknown reasons (Table 1). Detection probability of the downstream antennas was 79%, leading to an adjustment of 39 fish (see total adjusted in Table 1).

Total Number of Out-Migrants and Age Structure

The estimated number of Bull Trout out-migrants from Graves Creek was highest in the autumn of 2019 (Table 1). In autumn 2019, a total of 704 Bull Trout were captured and an estimated 843 (98) (mean [95% CI]) Bull Trout out-migrated (Table 1). The age-structure of Bull Trout captured in the trap was 71% age 1, 29% age 2, and <1% age 3 (Table 1). The estimated age structure of the total number of Bull Trout out-migrating was similar and was 72% age 1, 28% age 2, and <1% age 3 (Table 1). During the spring 2020 trapping season, 50 age-2 or older Bull Trout were captured in the trap, and the total estimated number of age-2 or older out-migrating Bull Trout was 472 (248) (Table 1). All of the previously tagged and aged Bull Trout that were subsequently captured in the trap or missed by the trap ($n = 86$) during the spring of 2020 were age-2 fish. Two age-1 Bull Trout were captured in the trap; however, we were not able to estimate the total number of age-1 out-migrants because age-1 Bull Trout were too small to tag prior to spring out-migration (Table 1). In autumn 2020, 616 Bull Trout were captured in the trap, and the total estimated number of out-migrating Bull Trout was 679 (38) (Table 1). The age structure of Bull Trout captured in the trap was 12% age 1, 87% age 2, and 1% age 3 (Table 1). The estimated age structure of the total number of Bull Trout out-migrating from Graves Creek was similar and was 11% age 1, 88% age 2, and 1% age 3 (Table 1). During the spring 2021 trapping season, 13 age-2 or older Bull Trout were captured in the trap and the total estimated number of age-2 or older out-migrating Bull Trout was 199 (121) (Table 1). Only one Bull Trout that was previously tagged and aged was captured in the trap and was age 2; however, of the 21 Bull Trout that were previously tagged and aged and missed by the trap, 9 were age 3 and 11 were age 2 (Table 1).

Timing of Out-Migration and Overall Efficiency of Downstream Trapping Methods

In Graves Creek, out-migration primarily occurred in four discrete events, and out-migration events coincided with the trapping seasons (Figure 3). In 2019 and 2020, a small number of Bull Trout out-migrated in the summer prior to the autumn trapping season; however, the majority of out-migration occurred during the autumn trapping seasons (Figure 3). During the autumn trapping seasons, the temporal distribution of out-migrating Bull Trout was similar for tagged fish captured in the trap and all tagged out-migrating Bull Trout (Figure 3). Minimal out-migration occurred during the winter (Figure 3). Although the spring trapping seasons coincided with out-migration events, few Bull Trout that out-migrated during the spring were captured in the trap (Figure 3). The magnitude of spring out-migration was lower in 2021 when compared to 2020; however, in both years, out-migration peaked in late April.

Of the 821 tagged age-1–3 Bull Trout, 41% (335) were confirmed to have out-migrated from July 2019 through July 2021 (Table 2). Fifty-two percent of out-migrating Bull Trout out-migrated during trapping seasons and were captured by the weir trap (Table 2). Thirty-seven percent of the tagged out-migrants were missed during trapping seasons and the majority were missed when the trap was known to be compromised due to conditions (Table 2). Eleven percent of the total number of tagged Bull Trout out-migrated during seasons when the trap was not fishing (Table 2). The average detection probability of antennas A1 and A2 during the summer seasons was 98%, and detection probability during winter seasons was 100%, making it unlikely that a tagged fish out-migrated when the trap was not fishing and was not detected. Based on the age distribution of out-migrating Bull Trout, some of the Bull Trout that were not detected out-migrating during the study ($n = 486$) may have out-migrated after the study concluded; however, the majority likely represent natural mortalities.

DISCUSSION

Establishing a representative population of tagged fish in Graves Creek enabled the use of PIT antennas to monitor out-migration year-round and highlighted how knowledge based on trap captures can be biased unless seasonal variability in capture efficiency is explicitly quantified. Our results indicated that the downstream trapping program in Graves Creek captured variation in age at out-migration and timing of out-migration of juvenile Bull Trout during the autumn trapping seasons. However, although the spring trapping seasons coincided with the timing of the spring out-migration events in Graves Creek, few spring out-migrating Bull Trout were successfully captured. Identifying the factors that contribute to fish being missed by the trap (i.e., age, season of out-migration) enables management actions to address potential sources of selectivity in the program and maximize variation within the population of transported Bull Trout. Conserving variation within life history strategies maximizes the chances of success for the downstream transport program and makes the Bull Trout populations more resilient in the future.

Seasonal variation in capture efficiency was substantial and contributed to a knowledge gap regarding juvenile Bull Trout out-migration dynamics in Graves Creek prior to this study. In other systems with adfluvial Bull Trout populations, juvenile out-migration has been observed to occur in two major peaks annually, once in the spring and once in the autumn (Hemmingsen et al. 2001; Downs et al. 2006; Ratliff et al. 2015). Prior to this study, only one major peak in out-migration was observed annually in Graves Creek based on trapping data and occurred in the autumn. When the temporal distribution of out-migration was plotted with only tagged Bull Trout that were captured in the trap during this study, a similar pattern was observed, with major out-migration observed only in the autumn. However, use of the PIT antennas revealed out-migration events from Graves Creek in the spring and autumn, and the spring out-migration event was masked by low capture efficiencies. Capture efficiencies in the spring were so low that traditional methods to account for

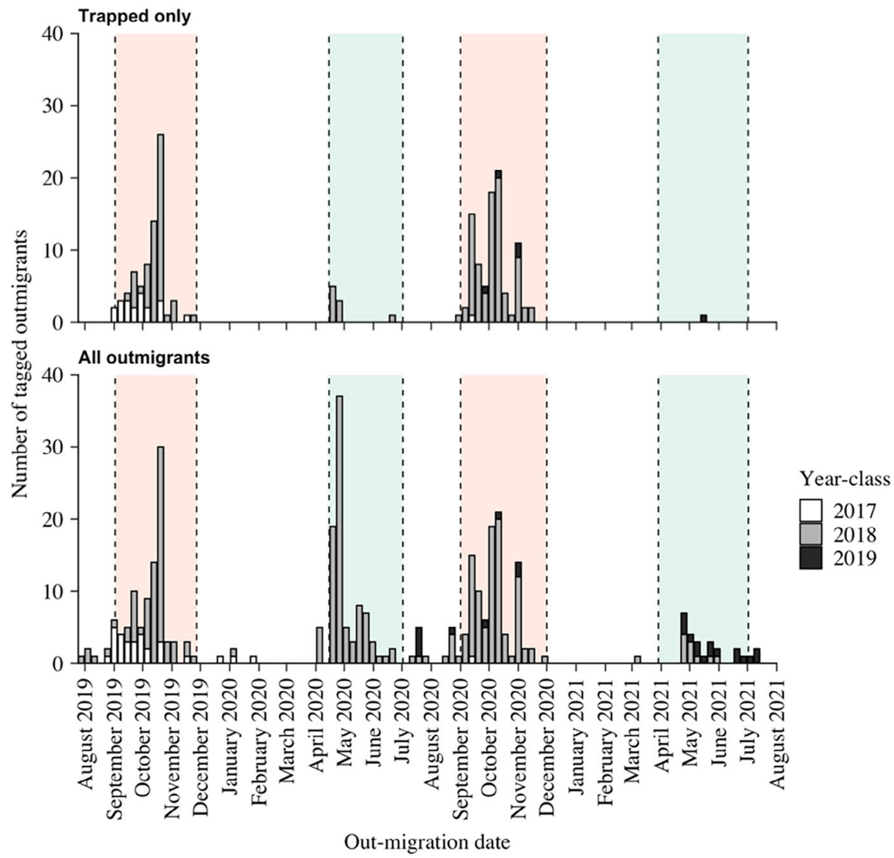

FIGURE 3. Timing distribution of tagged juvenile Bull Trout out-migrating from Graves Creek, Montana, with the top panel showing tagged Bull Trout captured in the permanent weir and the bottom panel showing all tagged Bull Trout detected out-migrating. The dotted lines and shaded areas depict the trapping seasons: autumn 2019 (September 4 to November 27, 2019), spring 2020 (April 15 to 2 July 2, 2020), autumn 2020 (September 2 to November 20, 2020), and spring 2021 (March 29 to July 2, 2021). The orange shading depicts autumn, and the green shading depicts spring. The gray shading within the bars depicts year-class.

TABLE 2. Fate of tagged Bull Trout out-migrating from Graves Creek, Montana, from July 2019 to July 2021, with fates defined as captured in weir trap, missed (unknown reasons), missed (not fishing or partially fishing due to holiday, weekends, or volitional passage), missed (trap compromised due to conditions), or missed (not fishing for the season).

Age at out-migration (*n*)	Trapped	Missed (unknown)	Missed (holiday, weekend, volitional)	Missed (compromised due to conditions)	Missed (out of season)
Age 1 (83)	59	11	1	0	12
Age 2 (237)	114	11	29	61	22
Age 3 (15)	2	1	0	9	3
All ages (335)	175	23	30	70	37

capture efficiency, such as releasing captured fish above the trap and determining the proportion recaptured (Volkhardt et al. 2007), would likely have failed to reflect the extent of the out-migration given that no tagged Bull Trout were trapped during the month of May in 2020 and only one previously tagged Bull Trout was captured in the spring of 2021. In the autumn trapping seasons, using the number of Bull Trout captured in the traps as a metric for total out-migration without accounting for capture efficiency would have underestimated total out-migration by 6–15% (based on 95% confidence intervals) in 2019 and 4–14% in 2020. In the spring of 2020, using the number of age-2 and older Bull Trout captured in the traps as a metric for total out-migration without accounting for capture efficiency would have underestimated total out-migration by 78–93%, and in the spring of 2021, the number of Bull

Trout captured in the traps would have underestimated out-migration by 83–95%. Therefore, seasonal variability in capture efficiency caused variation in the discrepancy between the number of Bull Trout captured in the trap and the total number of out-migrating Bull Trout.

In salmonids, variation in migration timing represents an important evolutionary trait that allows populations to be more resilient to stochastic environmental events by spreading the risk of migration over a longer period of time (Schindler et al. 2010; Moore et al. 2014). Thus, if trap-and-haul programs limit trapping to certain seasons based on conditions, or desirability of certain fish, the program could be selecting against variable life history timing (Kock et al. 2020). For example, if one were to trap spring out-migrating fish but only following the peak in spring discharge, early out-migrating fish would be selected against. Over time, this could lead to a loss of diversity in out-migration timing, making the populations less resilient in the future (Kock et al. 2020). The duration of the trapping seasons appeared appropriate to capture the majority of out-migrating Bull Trout from Graves Creek. Of the total tagged out-migrating Bull Trout, only 11% were missed due to out of season out-migration. However, despite the spring trapping seasons coinciding with the spring out-migration event, low trap efficiencies suggest that spring out-migrating Bull Trout are potentially experiencing negative selection.

Several factors can influence capture efficiency of the permanent weir, and increasing capture efficiency requires that these factors are identified. During the spring trapping season, most fish that were missed out-migrated when the trap was known to be compromised due to poor trapping conditions (i.e., the trap was overtopped with water because of high flows and high debris loads). Efforts to improve spring capture efficiencies could focus on increasing the ability of the trap to remain fully fishing through high flows. In the autumn 2019 trapping season, the majority of fish were missed for unknown reasons despite the weir appearing to be fishing to its fullest capabilities. Of the 12 fish missed for unknown reasons, 11 were age 1. Given the skewed age distribution, it is likely that the small age-1 Bull Trout were able to escape through gaps in or between weir panels on the trap. Capture efficiency for age-1 Bull Trout improved in autumn 2020; however, fewer age-1 Bull Trout out-migrated in the autumn of 2020 and only one Bull Trout <120 mm was captured in the trap in 2020, whereas 50 Bull Trout <120 mm were captured in autumn 2019. Therefore, the increased capture efficiency may have resulted from fewer small individuals out-migrating. Given that the minimum length to transport Bull Trout is 120 mm, size selectivity below this threshold will not influence the transport program; however, it is important to acknowledge this potential size selectivity when using the number of Bull Trout captured in the trap as a metric for total out-migration. The spacing on and between panels on the permanent weir was designed to minimize impingement while effectively capturing age-1 and older Bull Trout. Efforts to improve capture efficiency during the autumn trapping seasons could focus on minimizing potential spaces for escapement on the trap by adjusting the panel spacing or using netting to cover gaps.

The age-class structure of juvenile out-migrating Bull Trout can be variable among populations and can vary among years within a single population. In general, the majority of juvenile Bull Trout in adfluvial systems out-migrate between age 0 and age 3, with age-2 Bull Trout representing the majority of out-migrants, which was similar to what we observed in Graves Creek (Downs et al. 2006; Zymonas 2006). There is currently no evidence that Bull Trout out-migrating at age 0 survive in a lacustrine environment (Downs et al. 2006; Zymonas 2006; Ratliff et al. 2015), and we did not attempt to capture or enumerate age-0 Bull Trout. Despite variation in capture efficiency among ages during the autumn 2019 and autumn 2020 trapping seasons, the age-class structure of captured Bull Trout was reflective of the age-class structure of all out-migrating Bull Trout (indicated by the total number of out-migrants calculation). Therefore, we did not find evidence that the current autumn trapping methods were selecting against variation in age at out-migration. In the spring, we were limited in our ability to develop length-at-age relationships for trapped fish; therefore, we were only able to differentiate between age 2 and age 3 for fish that were previously captured and aged. During the spring of 2020, two age-1 Bull Trout captured in the trap during the spring did not meet the minimum length for transport (120 mm); therefore, spring trapping and transport efforts will likely continue to focus on age-2 and older Bull Trout. Larger size and older age at out-migration has been associated with substantial survival advantages for juvenile Bull Trout (Downs et al. 2006; Zymonas 2006; Oldenburg 2017); therefore, age-3 Bull Trout are particularly valuable to the transport program. The loss of these valuable older fish during the spring of 2021 may justify the use of additional resources to increase spring capture efficiency. Future research into the age of out-migration among returning adults would be valuable information for managing the trap-and-haul program.

The seasonal capture efficiencies in Graves Creek have implications for Bull Trout that use the reservoir system as a surrogate for lake habitat. Although the success (where success is defined as the probability of an out-migrating Bull Trout surviving to maturity and returning to their natal stream to spawn) of reservoir-type Bull Trout is hypothesized to be lower than that of Bull Trout transported to Lake Pend Oreille, past studies have found that reservoir-type fish do contribute to the Bull Trout population in Graves Creek (DeHaan and Bernall 2013). Variation in life history strategies is common in Bull Trout populations (Rieman and Mclntyre 1993; Al-Chokhachy and Budy 2008; Howell et al. 2016). Thus, reservoir-type fish may serve as an important buffer to variation in success of the two-way trap-and-haul program. However, it is possible that with increasing water temperatures and increased abundance of piscivorous nonnative species, over time the reservoir system could begin to act as an ecological sink (Nelson et al. 2002; Schlaepfer et al. 2002). With investments into infrastructure enabling the use of full-capture traps such as the permanent weir rather than partial-capture traps such as rotary screw traps, decisions will need to be made regarding whether a proportion of fish may be allowed to enter the reservoir or if all fish could be transported. Given the management implications, it is vital that the relative success of the reservoir-type Bull Trout be evaluated. Prior to this study it was unknown how many Bull Trout were entering the reservoir system, when they were entering the reservoir, and the age of the fish entering the reservoir. We found that autumn out-migrating Bull Trout are better represented in the transport program, whereas spring out-migrating Bull Trout are better represented in the reservoir system, where they may mature in the reservoirs or migrate volitionally downstream to Lake Pend Oreille. The number of tagged Bull Trout that out-migrated at age 2 over the course of the study that were captured was nearly equal to the number of age-2 out-migrating Bull Trout that entered the reservoir; however, the majority of age-2 Bull Trout that entered the reservoir entered during the spring; thus, they have a smaller body size relative to fall age-2 out-migrants that have an additional summer to grow. Additionally, 87% of age-3 out-migrants from Graves Creek entered the reservoir system. Timing of out-migration and size at out-migration have been identified as factors that influence the probability that Bull Trout will survive to maturity (Oldenburg 2017). Therefore, the information we collected will enable future efforts to compare the relative success of reservoir-type Bull Trout, volitional Lake Pend Oreille out-migrants, and transported Bull Trout while accounting for underlying factors that may influence survival based on characteristics of the Bull Trout that contribute to each life history strategy.

Although using PIT antennas offered several benefits when compared with traditional mark–recapture techniques, it can be challenging to classify fish as out-migrants based on detections given variable detection probability. Multiple factors can influence detection probability of PIT antennas, including environmental conditions, such as discharge or stage height, and characteristics or behaviors of the fish (Zydlewski et al. 2006). Placing multiple independent antennas or arrays in a stream can aid in the understanding of detection probability and enable direction of movement to be determined (Zydlewski et al. 2006; Connolly et al. 2008). We chose a semiconservative approach to classifying out-migration by considering fish as out-migrants if they were detected on at least one antenna downstream of the trap or captured in the trap. We subsequently adjusted our estimates of missed fish based on the probability that a fish may have passed both downstream antennas without being detected. While this method included a greater number of fish than if our protocol required directionality (i.e., detection on one upstream and one downstream antenna), the method excluded several fish that were only detected on an antenna located upstream of the trap. Classifying fish detected on any antenna as out-migrants would increase the probability of detecting out-migration (the probability of detection on any antenna exceeded 95% during all seasons); however, this method may overestimate out-migration because we cannot confirm that these fish passed downstream of the trap. Continued monitoring of detection probability under varying conditions and further investigation into the behavior of fish at and around the trap could enable more accurate estimates of out-migration. Adding an additional antenna on the downstream end of the trap could also increase the probability of tagged fish being detected as out-migrants.

An additional challenge associated with using PIT antennas and previously tagged fish to calculate capture efficiency is the lack of controlled sample size. Due to inconsistent sample sizes by week and month of each trapping season, we chose to stratify our estimates of the total number of out-migrants by age and season only. Using pooled data for a season may lead to bias in the estimate of the total number of out-migrating Bull Trout by season and may lead to underestimated variance in the estimates (Volkhardt et al. 2007). Achieving more accurate estimates by stratifying the data by week or month would probably require the incorporation of traditional mark–recapture efficiency trials to supplement the sample sizes of tagged out-migrating fish (Volkhardt et al. 2007).

Overall, our assessment of the downstream trapping efforts in Graves Creek indicated that Bull Trout transported during the autumn out-migration periods generally reflect the natural out-migration dynamics of the population. We also found that the current trapping seasons occur within the time periods of the major out-migration events, indicating little concern for selectivity against Bull Trout that may out-migrate outside of these time periods. However, the low capture efficiencies in the spring suggest that a disproportionate number of the spring out-migrants are not transported. Depending on the relative success of fish that are not transported, spring out-migrating Bull Trout may experience negative selection over time. Research into the demographic and genetic characteristics of spring out-migrating Bull Trout for a longer duration of time is needed to understand the relative importance of this currently underrepresented group of out-migrants in the trap-and-haul program.

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