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ARTICLE

# Movement Dynamics and Survival of Stocked Colorado River Cutthroat Trout

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***Abstract***
**The ability of native fish to establish self-sustaining populations when reintroduced to vacant habitats is variable. We evaluated factors that potentially affect the reintroduction success of juvenile Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus* that were reintroduced to an isolated watershed and were experiencing suboptimal survival and recruitment. We conducted a 3-year mark–recapture study to model annual apparent survival probability as it related to (1) different ex situ rearing strategies and (2) initial release among different habitat types. The use of PIT tags also enabled the quantification of loss via emigration. Apparent survival was highest for small fish that were minimally exposed to ex situ rearing conditions, stocked in small, headwater stream reaches. However, maximum estimates of apparent survival remained low ($\leq 0.38 \pm 0.05$ [estimate $\pm$ SE]) regardless of rearing treatment, stocking location, or interactive effects between covariates. Emigration of stocked fish (<1%) from the study area did not appear to limit their establishment. Our results suggest that variation in stocking and rearing strategy may have some effect on translocation success and the interaction between rearing and stocking strategy highlights the importance of considering the life history stage of stocked individuals when identifying stocking sites. Consistently low annual survival values may be indicative of a larger issue, requiring in-depth evaluation of adaptive potential within our brood source and other factors that potentially limit population persistence.**

Translocation of rare fish species has been widely adopted among fisheries managers as a strategy for promoting species viability (Williams et al. 1988). Translocation efforts may include new introductions, reintroduction, or supplemental stocking to bolster an existing population (Vincenzi et al. 2012). However, over 40% of translocations are thought to be unsuccessful (Cochran-Biederman et al. 2014). There is often insufficient monitoring and evaluation following the release of individuals to determine the reason for failure (Minckley 1995; Novinger and Rahel 2003).

One common translocation approach is isolation-reintroduction management, which is often employed when hybridization or resource competition with nonnative species is a concern (Kruse et al. 2001; Young and Harig 2001; Novinger and Rahel 2003; Young et al. 2005). This strategy involves building a fish barrier, eradicating nonnative fishes from the now isolated watershed

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via chemical or mechanical treatments, and reintroducing the desired species from either a captive or wild population. Isolation-reintroduction management is often used to mitigate declines in native salmonids in western North America (Behnke 1992; Thurow et al. 1997; Novinger and Rahel 2003; Andrews et al. 2013), where their occupancy of headwater habitats makes it a practical solution (Young 1995; Peterson et al. 2004; McGrath and Lewis 2007; Muhlfeld et al. 2009; Cook et al. 2010).

Because such projects are labor intensive and expensive, it is important to understand the factors that affect the reintroduction success of salmonids. Research has focused on habitat characteristics, including temperature regime, stream fragment length, total watershed area, and channel geometry characteristics (Harig et al. 2000; Harig and Fausch 2002; Roberts et al. 2013). Factors related to rearing history and stocking strategy of source populations such as size and age at stocking, time of stocking events, and duration of hatchery rearing have also been of interest (Cowx 1994; Griffiths and Armstrong 2002; Hilderbrand 2002; Augustyn et al. 2006). However, few studies have looked at both when quantifying reintroduction success.

We evaluated short-term reintroduction success of Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus* (CRCT) in an isolated watershed from which nonnative fish had been removed. Successful reintroduction requires that not all individuals emigrate from the isolated system poststocking and that residents survive to establish a self-sustaining population. Relative to these requirements, our objectives were to (1) quantify emigration out of the study area for reintroduced CRCT and (2) quantify apparent survival as it related to varying stocking and rearing treatments and habitat attributes. We predicted that treatments minimizing exposure to ex situ rearing facilities would yield higher estimates of survival (Johnsson et al. 2014; Stringwell et al. 2014). However, stocking larger fish could alleviate the initial energetic demands that are associated with acclimation to wild habitats. We further predicted an interaction between stocking treatments and habitat, with younger, age-0 individuals benefiting from initial introduction to smaller headwater reaches (Rosenfeld et al. 2000).

## METHODS

We conducted an intensive 3-year mark–recapture study to monitor emigration and estimate survival probabilities for multiple stocking and rearing treatments of a sole source population released in different habitats. We evaluated the effects of seven treatments, which varied in hatchery time, fish size, and age at stocking, on survival probability.

*Study site.*— We conducted this study in LaBarge Creek (HUC-10), a tributary of the upper Green River drainage in western Wyoming (Figure 1). LaBarge Creek was selected by the Wyoming Game and Fish Department (WGFD) in 1999 as an isolation-reintroduction management site to establish a genetically pure, self-sustaining CRCT population because of its size and historical use by CRCT (Hirsch et al. 2013). Barrier construction and eradication efforts resulted in approximately 93 km of available habitat by 2006. Despite repeated stocking since 2007 (16,000–48,000 fish were stocked per year from 2008 to 2014; Figure A available in the Supplementary Material in the online version of this article), the establishment and reproduction of CRCT remained minimal. Backpack electrofishing surveys found 0.2–1.5 fish/100 m (WGFD, unpublished data). It is unclear what factors have limited establishment and reproduction. The drainage has no agricultural or residential land use but has been subject to livestock grazing practices since as early as 1857. However, the removal of over 28,000 fish, 62% of which were salmonids, during treatment suggests that potential habitat degradation that is often associated with grazing has not hindered desirable fish densities in the recent past (WGFD, unpublished data). LaBarge Creek drainage is a good location for evaluating translocation success because of the currently low fish densities, continued exclusion of nonnative fishes, and amount and diversity of available habitat that is encompassed.

The fish that were used for reintroduction were manually spawned from a wild population in North Piney Lake NAD83 12N 534874, 4721922 located 14.62 km (linear distance) from LaBarge Creek. Previous screening conducted by the WGFD deemed this population sufficiently void of genetic impurity and disease. Fertilized eggs were sent to one or two of three WGFD rearing stations where they were reared for varying times prior to stocking. The fish that were sent to the Boulder rearing station (Boulder Rearing Station Road, Boulder, Wyoming) were reared in outdoor concrete raceways. The fish that were sent to the Dan Speas rearing station (Speas Road, Casper, Wyoming) were reared in indoor fiberglass raceways. The fish that were sent to the Daniel rearing station (Pape Road, Daniel, Wyoming) were reared in indoor concrete raceways. All of the rearing stations are spring-fed, receiving water at constant mean temperatures of 10.56°C, 15.56°C, or 7.22°C, respectively.

*Tagging techniques.*— To quantify the emigration and survival rates of CRCT, we PIT-tagged 6,953 fish that were representative of seven distinct stocking and rearing treatments, 23.3% of the 29,880 fish that were stocked in 2015 and 2016 (Table 1). The codes that were used to define each treatment were fish age, rearing station(s), and month stocked (e.g., 1D8 indicates age-1, reared at Daniel and stocked in August). Three of the treatments (1D8, 1D9, and 0S10) were replicated in 2015 and 2016, but this was not feasible for all of the treatments because of

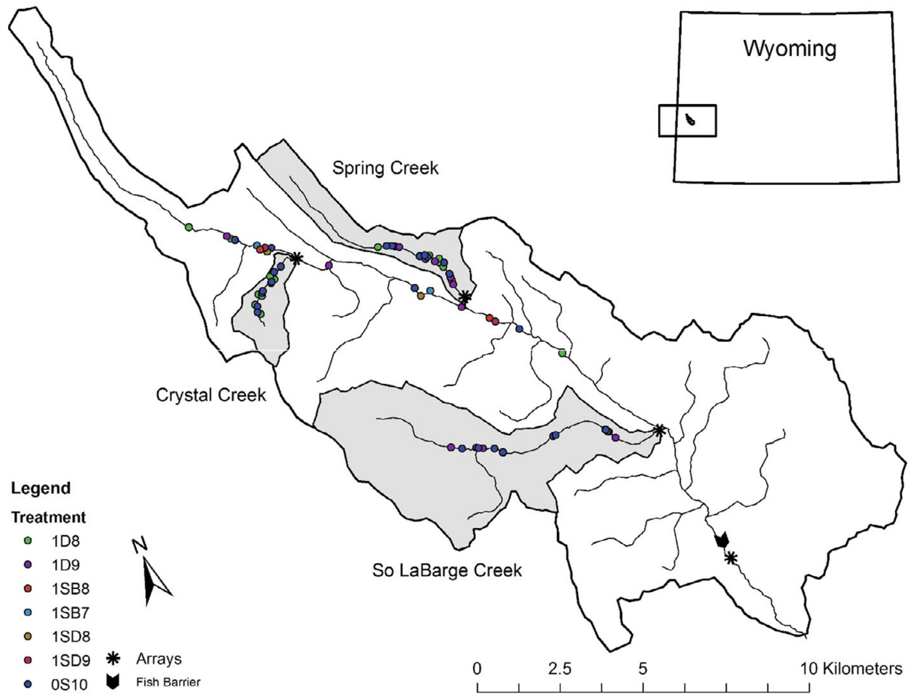


FIGURE 1. Stocking locations for each rearing treatment that was employed in LaBarge Creek drainage (2015–2016) in relation to stationary PIT antenna array locations and the fish migration barrier. Main-stem stock sites of the same treatment are reduced to a single point within 500-m release locations to increase clarity. Overlapping points were offset from the stream to increase clarity. All of the fish that were detected at the array below the fish barrier were classified as permanent emigrants from the system and removed from subsequent survival analysis. The treatment codes are explained in Table 1.

TABLE 1. Stocking and rearing treatments employed in LaBarge Creek drainage from 2015 to 2016. The first digit in the treatment codes signifies age at stocking (years), followed by initial(s) of rearing station(s) and ending in month stocked. Treatments 1SD8, 1SD9, 1SB7, and 1SB8 could not be replicated during both years of the study. All of the batch weights (fish/kg) were provided by WGFD hatchery personnel at the time of stocking. Lengths (mm) were recorded during tagging prior to releasing the fish.

| | Treatment | Rearing station(s) used | Age | Stock date (mm-dd) | Months reared | Fish/kg | Mean length (mm) | LaBarge # tagged | So. LaBarge # tagged | Spring # tagged | Crystal # tagged |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2015 | 1D8 | Daniel | 1 | 08-06 | 14 | 15.42 | 113.2 | 294 | | 251 | 251 |
| | 1D9 | Daniel | 1 | 09-09 | 15 | 11.33 | 122.4 | 277 | 269 | 248 | |
| | 0S10 | Speas | 0 | 10-05 | 4 | 31.75 | 86.0 | 599 | 301 | 249 | 246 |
| | 1SD8 | Speas/Daniel | 1 | 08-07 | 14 | 3.18 | 190.9 | 246 | | | |
| | 1SD9 | Speas/Daniel | 1 | 09-10 | 15 | 3.04 | 196.3 | 249 | | | |
| 2016 | 1D8 | Daniel | 1 | 08-04 | 14 | 12.70 | 124.1 | 297 | | 246 | 247 |
| | 1D9 | Daniel | 1 | 09-07 | 15 | 9.07 | 131.4 | 248 | 253 | 248 | |
| | 0S10 | Speas | 0 | 10-11 | 4 | 44.63 | 79.8 | 580 | 289 | 245 | 244 |
| | 1SB7 | Speas/Boulder | 1 | 07-14 | 13 | 3.76 | 178.8 | 247 | | | |
| | 1SB8 | Speas/Boulder | 1 | 08-12 | 14 | 3.22 | 186.8 | 247 | | | |

logistical constraints in the hatchery system. Thus, treatments 1SD8 and 1SD9 were only stocked in 2015 and 1SB7 and 1SB8 in 2016.

All of the tagging was done at WGFD rearing stations prior to stocking. Individuals were anesthetized using AQUI-S 20E, measured, and PIT-tagged. We implanted the fish that were 79.8–131.4 mm TL with 12-mm half-duplex (HDX) PIT tags and those that were 178.8–196.3 mm TL with 23-mm HDX PIT tags (Oregon RFID, Portland, Oregon). We implanted the tags in the peritoneal cavity using injection guns that were fitted with Luer lock needles (Oregon RFID). We held the fish in the hatchery system 4–24 d prior to stocking to assess tag retention and mortality (Table B1 available in the Supplementary Material in the online version of this article). Because of the high retention rates that we observed in the hatchery and small size of fish used in this study, we did not double-mark individuals to test tag retention. Additionally, it was unlikely that tag loss occurred after stocking because although tags can be expelled during spawning (Bateman et al. 2009), the fish did not reach reproductive age (4–5 years; Downs et al. 1997) during the study period.

*Fish stocking.*— Following the survival and tag retention evaluation, we stocked the fish at locations throughout the main-stem LaBarge Creek (128 sites) and three tributaries: Crystal Creek (16 sites), Spring Creek (24 sites), and South LaBarge Creek (16 sites) during August–October 2015 and July–October 2016 (Figure 1). The fish treatments were evenly allocated between sites except that all larger fish (>175 mm) were distributed only among main-stem locations. We scanned the fish by using handheld HDX proximity readers (Oregon RFID) immediately prior to stocking to discern the release locations of individuals. The main-stem stocking sites were predetermined based on the prevalence of pool habitat. We could not access the tributary stocking sites by road, so the fish were backpacked to the stocking locations. To reduce initial competition among the fish that were stocked in tributaries, the crews were instructed to select stocking sites based on timed hiking intervals. The fish were carried upstream for 15, 20, 30, and 45 min on each tributary per stocking treatment. Once the crew members had hiked for the duration of their designated time, they were instructed to locate the nearest pool complex and release the fish. The stocking locations were recorded using handheld GPS units (GPSMAP 64s, Garmin Ltd., Olathe, Kansas).

*Emigration and survival data collection.*— We assessed the emigration and survival rates of the PIT-tagged fish by using mobile backpack PIT antenna units and stationary instream antenna arrays from May 27 to November 26, 2016, and June 19 to October 10, 2017. We conducted mobile PIT tag surveys using low-frequency backpack RFID reader-data loggers that were equipped with PVC antenna wands and internally housed slim-tuners (Oregon RFID). We tuned the readers prior to each sampling event to ensure a maximum vertical read range of approximately 0.43 m for a 12-mm tag and 0.90 m for a 23-mm tag. We slowly and systematically moved in an upstream direction at predetermined reaches, scanning the entire wetted width and water column. Once we detected a tag, we recorded its identification number, coordinates (Universal Transverse Mercator Zone 12, North American Datum 83), and whether the fish was alive or dead. To distinguish between live and dead individuals, we first looked for a possibly tagged fish. If we did not see one, the area where the tag was detected was vigorously disturbed for a minimum of 10 s and rescanned. Because we assumed 100% tag retention, if the tag remained sedentary, it was defined as a mortality. For the analyses, we assumed that dead fish were correctly identified, which is supported by data-proofing exercises.

Due to the potential for high mortality, low densities, and patchy distribution of juvenile CRCT, we wanted to maximize the number and length of the mobile PIT survey reaches given time limitations and crew availability. We sampled all of the stocked tributaries from the confluence to the farthest upstream 2015 stocking location. For LaBarge Creek, we selected six 500-m main-stem reaches. We randomly selected four sites based on stocking locations: one site that was representative of canyon habitat and one site below our farthest downstream stocking site to increase recapture rates in the event of downstream dispersal of individuals. We sampled all of the reaches three times per year from late June to early October in 2016 and mid-July to early October in 2017. We blocked off all of the sites to prevent movement out of reaches during sampling and used two backpack units for reaches with mean wetted widths ≥2 m to increase detection efficiency.

We constructed stationary instream antenna arrays at the confluence of each tributary to collect ancillary recapture data between discrete mobile sampling events. An additional array was constructed 65 m below the fish migration barrier to quantify permanent emigration from the system (Figure 1). Two single arrays were used at each site so that we could determine direction of travel. Each array consisted of a pass-through antenna, a standard remote tuner board that was housed in a water-resistant box, and a low-frequency single HDX RFID reader (Oregon RFID). We downloaded data from all of the readers weekly.

We tested the arrays for detection efficiency weekly by passing a 12-mm HDX PIT tag perpendicular through the array at equidistant intervals. If we detected gaps in the antenna, it was retuned using a HDX tuning indicator (Oregon RFID). The arrays remained operational throughout the sampling periods except for brief periods when maintenance was required. The array that was located on Crystal Creek in 2016 provided one exception, operating for 1,346.5 out of 1,706.5 sampling hours due to a faulty charging system.

Because we could not maintain the arrays throughout the winter, we conducted additional mobile surveys below the fish barrier in 2017. Supplemental sampling efforts below the barrier allowed the opportunity to recapture any individuals that may have emigrated while the arrays were not operational. We sampled one 500-m reach directly below the barrier and randomly selected another five 100-m reaches within the 3 km that were accessible above a private land boundary.

*Habitat data collection.*— We measured a suite of habitat characteristics that is associated with survival and recruitment of CRCT to determine whether differences in habitat quality or quantity between stocking sites affected the survival of this species. We recorded temperature data hourly using HOBO 8K Pendant temperature loggers (Onset Computer Corporation, Bourne, Massachusetts) from early spring 2016 to late fall 2017. We had three sites on the main stem (2,361, 2,464, and 2,587 m in elevation from downstream to upstream) and sites at the upper and lower bounds of each stocked tributary based on the farthest downstream and upstream stocking locations in 2015. We calculated maximum 30-d average temperature (M30AT) metrics, which are believed to be the most relevant to CRCT growth and recruitment (Roberts et al. 2013).

We established four stream discharge monitoring stations: on the main stem below the fish migration barrier and at the confluence of each stocked tributary. We took cross-sectional depth and flow (at 60% of depth) measurements at 7–11-d intervals throughout both field seasons using a Hach FH950 flow meter (Hach Company, Loveland, Colorado) and a stadia rod. Due to safety concerns, we were not able to measure flow during peak discharge events in the spring.

We collected data on physical stream characteristics at four of the 500-m reaches that were used in mobile PIT sampling on the main stem and one 300-m reach in each study tributary. We conducted habitat surveys within large, predetermined reaches because measuring stream scale habitat metrics that may affect the persistence of CRCT often involves quantifying the abundance of a single geomorphic channel unit (e.g., pool habitat) and its characteristics (Harig and Fausch 2002; Young et al. 2005) and large reaches were necessary to encompass multiple pool habitats. We recorded wetted width, bankfull width, mean depth, thalweg depth, substrate characteristics, and overhanging riparian vegetation data at 11 equidistant transects for all of the reaches (Table C).

*Habitat analysis.*— We performed the statistical analyses using Program R (R Core Team 2016, version 3.3.2). We calculated the habitat metrics that are hypothesized to influence CRCT survival for each reach, flow station, and temperature-monitoring station in 2016 and 2017. We only conducted beaver pond counts in 2017; however, 72% of the impoundments were classified as inactive (absence of green woody debris), so the data were considered representative of the sites prior to sampling. We calculated substrate diversity using Shannon's diversity index with the "diversity" function in the "vegan" package (Oksanen et al. 2018).

We did not measure habitat variables during the 2015 stocking events, so time-varying habitat covariates could not be included in the survival models. To account for this, we assumed that 2-year (2016, 2017) mean habitat metrics were representative of individual sites across time for the duration of this study. To test these assumptions, we compared differences in habitat metrics between 2016 and 2017 using a pairwise Student's $t$-test or a Wilcoxon rank-sum test depending on whether the data met assumptions of normality. Because the sites exhibited no statistical difference in habitat metrics between years or homogeneously increased or decreased across sites, we believe 2-year means to be a reasonable representation of habitat variability among sites for all metrics.

Once the mean habitat metrics were derived for all of the sites, we used principal component analysis (PCA; Zuur et al. 2007) to reduce potentially correlated variables to singular components by using a correlation matrix with package "vegan" (Oksanen et al. 2018). We used the first two principal components (PC1, PC2) as covariates indicating habitat conditions at stocking sites in survival models. We used M30AT values as our temperature covariate in the eventual survival models. Temperature was not included in the PCA because we measured temperature at a differing spatial scale to capture the longitudinal gradient in temperature regime throughout the watershed. Route network analysis was employed using ArcGIS (ESRI 2014) to assign the fish to their associated PC1, PC2, or M30AT value based on the closest stream network distance of habitat-monitoring sites to the respective stocking locations within the drainage where they were introduced.

*Survival analysis.*— We estimated annual apparent survival probability ($S$) using Pollock's (1982) robust design mark–recapture model (Figure 2). Survival is termed "apparent" because movement out of a sampling reach cannot be distinguished from mortality. Therefore, we acknowledge that fish movement to unsampled reaches within the LaBarge Creek study area could negatively bias the survival estimates. The analyses were conducted in program MARK (White and Burnham 1999), with models constructed in the "RMark" package (Laake 2013) in R. Several factors that were specific to our study scheme required modification of the standard robust design. First, encounter histories for each fish began when they were stocked and thus introduced to the system. Therefore, we distinguished between initial capture probability, $p$, which was constrained to 1 during the sampling occasion when an individual was stocked, and recapture probability, $c$, which included poststocking sampling occasions and surveys after the initial capture of an individual in a given year. Second, stocking began in 2015; however, recapture

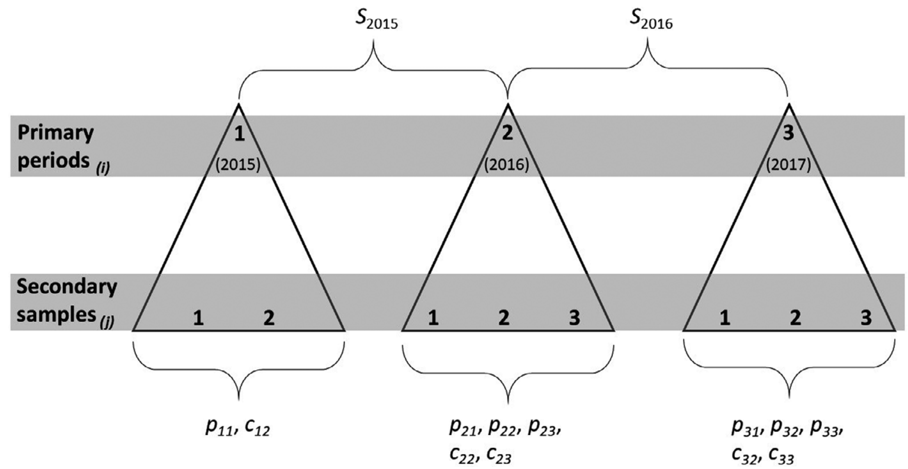


FIGURE 2. A conceptual diagram of Pollock's (1982) robust design relative to our study scheme. The probability of initial capture ($p_{ij}$) and the probability of recapture ($c_{ij}$) are estimated for each primary period ($i$), using closed population models where $j$ indexes the number of trapping sessions (secondary samples) within that primary period. Survival probability ($S$) is estimated for intervals between primary periods when the population is assumed open. For fish stocked in 2016 (e.g., during sample 1), primary period 1 initial capture ($p_{11}$) and recapture ($c_{12}$) probabilities were fixed at 0 because those individuals were unavailable for capture during that time. Because we stocked fish in 2015 and did not conduct recapture surveys until 2016, trapping session 2 during the first primary period denotes a dummy session, where $c_{12}$ was fixed at 0 to account for no sampling effort.

efforts did not ensue until the following year (primary period 2; Figure 2). To account for the absence of recapture effort, a dummy secondary sampling session was added following all of the release events in 2015 and recapture probability was constrained to $c = 0$ during that session. Third, stocking treatments were replicated during 2016, thereby increasing the population during closed sampling efforts. To account for closed population model assumptions, initial capture and recapture probabilities were constrained to $p = 0$ and $c = 0$ prior to an individual's introduction to the system. Given that we only had two true primary periods containing recapture data postrelease, estimates of temporary emigration ($\gamma'$, $\gamma''$) became inestimable and confounded with survival. Thus, a limitation of our model was that these parameters had to be fixed to 0 and dropped from analysis. Individuals that permanently emigrated off the study area (i.e., moved over the fish barrier and were detected at the array) were removed from the survival analysis following the emigration event.

Our first primary period encompassed all of the 2015 stocking events (i.e., initial captures) from August to October 2015. Primary periods two and three occurred from the first day recapture efforts began to the last day that they were conducted in each field season (May–November 2016, June–October 2017). Within each primary period, secondary sampling events were defined as the intervals during which all nine mobile PIT reaches were sampled one time. In total, we conducted three secondary sampling efforts per year (every 6–8 weeks from June/July to early October) in 2016 and 2017. We assigned stationary antenna array data that were collected above the barrier during a given secondary sampling effort to that respective time interval. Because we were interested in estimating annual survival rates, we were able to assign ancillary recapture data that were collected between secondary periods to the following secondary period without temporally biasing the estimated survival rates. The use of stationary antenna detections in the model redefined recapture probability ($c$) as the joint probability of recapture via mobile PIT surveys and or stationary arrays.

Rather than fitting an extremely large model set incorporating all of the plausible combinations for the model parameters, we adopted a step-down approach (Lebreton et al. 1992) to identify the supported models for survival. We held $S$ at a high complexity (survival varied by year and treatment) while identifying the most parsimonious structure for capture probability (Doherty et al. 2012). We hypothesized that capture probability would decrease in deeper, wider channels (i.e., decrease along a headwater–main-stem gradient). However, because we obtained field-derived habitat metrics at a subset of reaches that we surveyed, we did not have corresponding habitat (e.g., mean depth) values for every capture location. Therefore, we matched values from the National Hydrography Dataset Plus High Resolution (Moore et al. 2019) to the spatial location ($x$, $y$ coordinate) where a fish was captured to reflect the environmental conditions at the capture locations more accurately. We used this metric to represent total upstream cumulative drainage area (UDA) from each capture location. Upstream drainage area typically correlates well with stream order/magnitude (Hugueny et al. 2010), as was the case in our system (UDA and Strahler stream order had a correlation coefficient of 0.79). Therefore, UDA represented a continuous headwater–main-stem gradient that we used as a covariate on both capture/recapture and survival probability. Further, because some fish moved within our system, the UDA values varied depending on the location where an individual was recaptured. Therefore, we used an extension of the robust design, the Huggins estimator, which permits capture and recapture probabilities to be modeled as functions of individual, time-varying covariates (Huggins 1989).

We ran models in which capture probability varied by primary period (i.e., year), secondary sampling occasion, treatment, and UDA values, including additive and interactive combinations of these variables. For each model structure, we evaluated models in which initial capture probability and recapture probability were estimated separately ($p \neq c$) and models with one parameter for capture probability ($p = c$; achieved via "sharing" parameters in RMark). Retaining the most parsimonious structure(s) for capture probability, we then addressed our hypotheses with respect to survival. We ran models in which apparent survival varied by year, treatment, and habitat covariates (PC1, PC2, UDA, M30AT), including additive and interactive combinations of these variables.

During each step of the modeling procedure described above (i.e., capture probability, apparent survival), we dropped the models that did not converge or models with singular parameters. We used Akaike's information criterion adjusted for effective sample size ($AIC_c$) for model selection, where models exhibiting $\Delta AIC_c$ of 0–2 were considered to have substantial support (Burnham and Anderson 2002). To our knowledge, there is currently no robust goodness-of-fit test for assessing the fit of open population models. To address fit, we manually fixed the variance inflation factor, or overdispersion parameter to $(\hat{c}) = 1$, indicating a perfect fit to the data. We then increased $\hat{c}$ to 2 by increments of 0.25 and assessed changes to the $QAIC_c$ rankings (Burnham and Anderson 2001). If the most parsimonious model prior to increases in $\hat{c}$ sustained $\Delta QAIC_c < 2$ throughout all of the manipulations, we assumed a conservative level of confidence regarding model fit.

## RESULTS

### Movement Patterns

Of the 6,871 individuals stocked, 7 were observed permanently emigrating from the system during 6,044 cumulative hours of stationary array operation during 2016–2017. Additional mobile surveys that were conducted below the fish barrier in 2017 resulted in four more detections, all of which were classified as mortalities.

Movement patterns within LaBarge Creek drainage, above the fish barrier, varied by year and subdrainage (Figure 3). In total, 224 (3.3%) individuals were observed moving out from the tributaries where they were stocked or were located outside of the tributary. Movement into the tributaries was less, with 66 individuals (<1%) entering subdrainages differing from their initial stocking location. Most movement events (74.8%) were observed during the same year that an individual was stocked (Figure 3). Spring and Crystal creeks showed the highest number of movements out of the tributary across years ($n_{\text{spring}} = 178$; $n_{\text{crystal}} = 39$).

### Habitat Attributes

Water temperatures varied between sites and seasonally, with June to November temperatures ranging from 1°C to 14°C; July and August were the warmest months. The M30AT values ranged from 5°C to 13°C and were generally higher in 2016 than in 2017. Discharge in Crystal and Spring creeks was consistently low (<1 $m^3$/s), while South LaBarge and LaBarge creeks showed a spring snowmelt peak, with maximum discharge rates of 3 and 8 $m^3$/s, respectively, in 2016. During 2017, peak discharges were likely substantially higher because high sustained spring flows in 2017 prevented the deployment of loggers until after peak flow.

The first two components (PC1, PC2) of our PCA model explained 87.9% of the total variance in the habitat metrics that were measured for each site (69.9% for PC1, 18.1% for PC2; Figure 4). The most important loadings on PC1 were channel geometry and flow characteristics. The sites with higher PC1 values showed a consistent increase in geometric channel dimensions, had greater minimum and mean discharges, a lower degree of variation around mean discharge, and decreased pool cover and overhanging riparian vegetation. We interpreted PC1 as a gradient from headwater to main-stem sites, with headwater sites potentially indicative of juvenile refuge-rearing habitat and main-stem sites as larger, mature fish habitat. The most important loadings for PC2 included deep pool and pool abundance (Figure 4), which may indicate suitable overwinter habitat between different sites. Thus, the values for PC1 and PC2 were included as covariates in the candidate models for estimating survival. We did not include PC1 and PC2 as covariates when modeling capture/recapture probability, as those values were more indicative of initial stocking location (which we were interested in with respect to survival) than actual capture location.

### Recapture of Marked Fish

Tag retention and survival remained high (>97%) across all of the treatments at the time of stocking

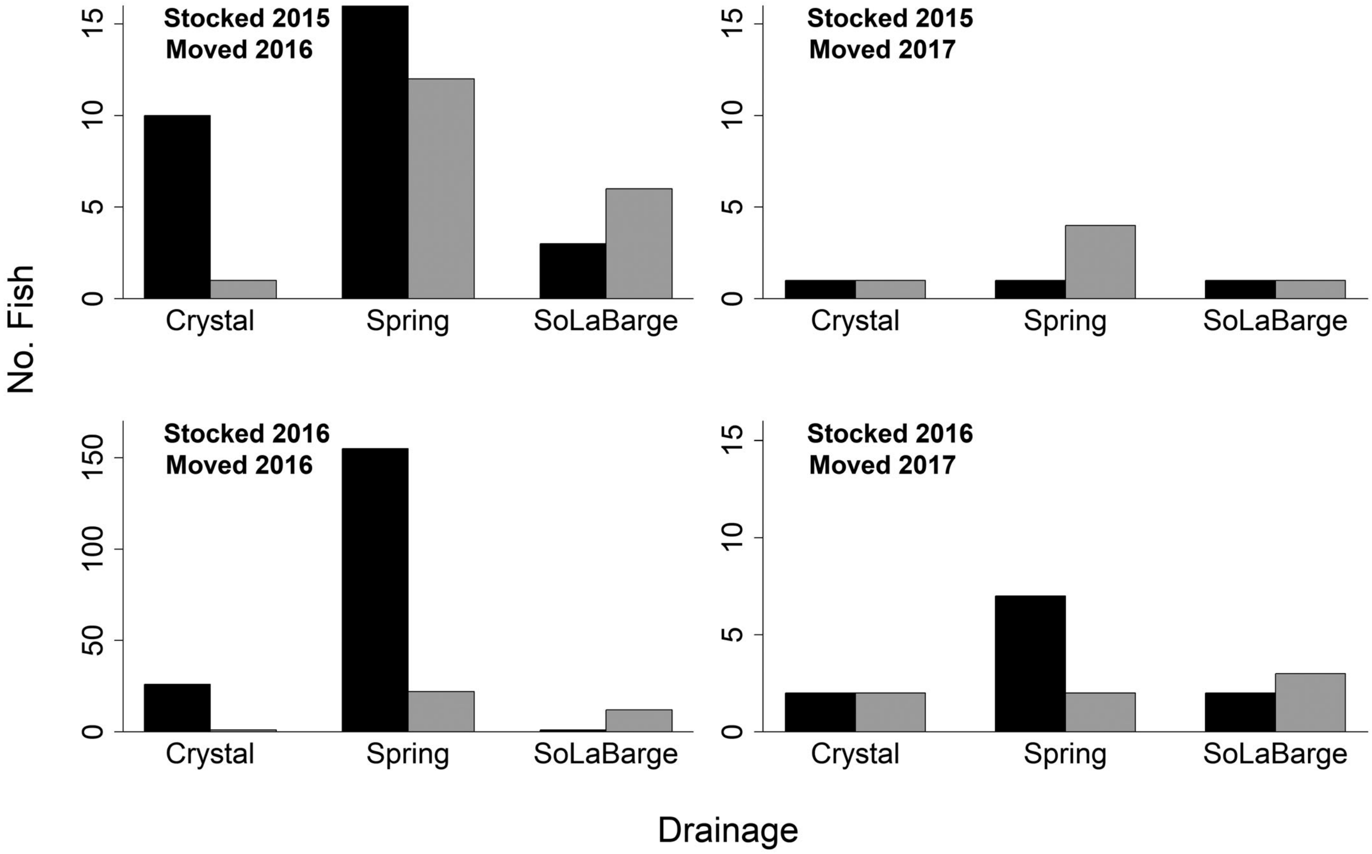


FIGURE 3. Movement events occurring 1–2 years poststocking for fish that were stocked in 2015 (top row) and the same year as stocking versus 1-year poststocking for fish that were stocked in 2016 (bottom row). Movement was defined as exiting (black) the subdrainage in which the individual was initially stocked or entering (gray) a different subdrainage. All of the events occurred above the fish barrier and thus do not indicate permanent emigration from the system. Note the differences in scale of the *y*-axis between panels. Movement events were considerably fewer 1–2 years poststocking when compared with events that occurred during the same year that the fish were stocked.

(Table B1). In total 6,871/6,953 (98.8%) of all of the fish that were tagged both retained their tag and survived to the time of stocking. Live recaptures for treatments 1SD8, 1SD9, 1SB7, and 1SB8 all ranged from 0 to 2 fish the year after they were released (Table B2). Due to the lack of recapture data, we dropped these treatments from the survival analysis. The stationary array data accounted for approximately 25% of all of the live detections, and mobile PIT data provided approximately 75%.

We found no evidence of overdispersion ($\hat{c} = 0.96$) in our most general robust design capture–recapture models and thus used AIC$_c$ to compare the models and calculate model weights. The best-supported model for capture and recapture probability (model weight, $w = 0.93$) included the additive effect of UDA and secondary sampling session for capture probability and the additive effect of UDA and treatment for recapture probability (Table 2). Capture probability ($p$) ranged from 0.14 to 0.27 and decreased temporally within each primary period (e.g., May–November). Recapture probability ($c$) was both highest (0.46) and lowest (0.17) in the 1D8 treatment for fish that were stocked in 2015 versus 2016, respectively (Table 3). Initial capture probability and recapture probability were both negatively correlated with UDA ($p$, $\beta_{\text{UDA}} = -0.02$ [SE = 0.006]; $c$, $\beta_{\text{UDA}} = -0.02$ [SE = 0.004]).

## Annual Survival Probability

The best-supported model for survival probability (model weight, $w = 0.90$) included the interactive effect of treatment and PC1 and sustained a $\Delta$QAIC$_c = 0$ through all incremental of the increases to $\hat{c}$. Survival decreased as PC1 values increased (i.e., stocking locations moved from headwaters to main stem) for all treatments and replicates (2015 and 2016), but the extent of the decrease varied by treatment and replicate (Figure 5). Treatment 0S10 produced the highest mean survival estimates; however, when stocked in 2016, 0S10 did not differ statistically from the other treatments (the 95% confidence intervals overlapped; Figure 6). Moreover, fish from treatment 0S10 that were stocked in 2015 into sites with

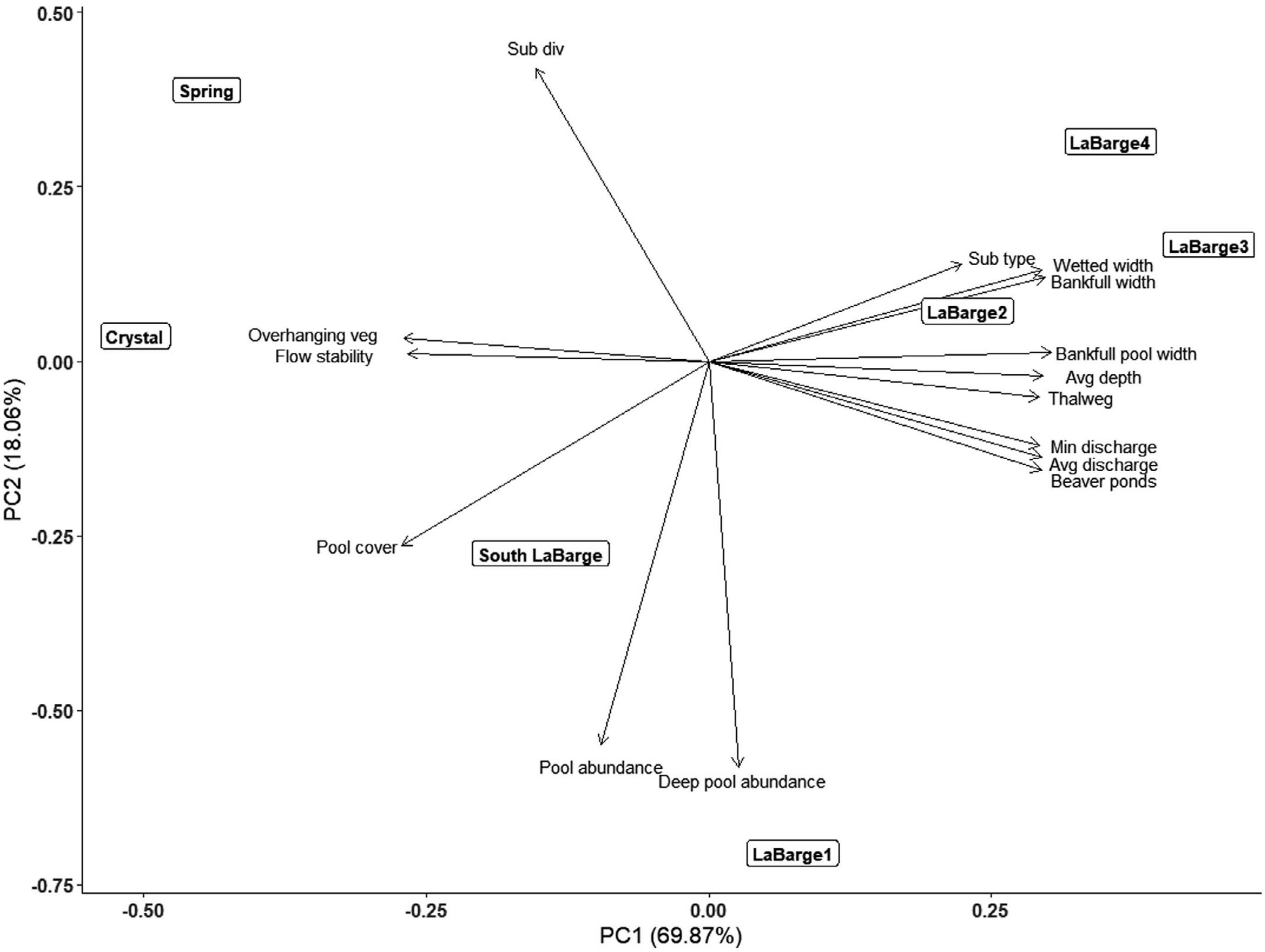


FIGURE 4. Principal component analysis (PCA) of mean annual habitat metrics in relation to sites where fish were stocked. The PC1 values from low to high indicate a gradient of fluvial geomorphic habitat conditions, with low PC1 values indicating headwater habitat and high PC1 values indicating spatially larger main-stem habitat. Low PC2 values indicate higher prevalence of deep pools (residual depth ≥30 cm) and pools (residual depth ≥18 cm) and were considered an index of overwinter habitat abundance. LaBarge sites 1–4 refer to their position in the watershed, with 1 representing the farthest upstream.

the lowest PC1 scores exhibited the highest potential for annual survival probability ($S = 0.38$ [SE = 0.05]) and sustained greater survival estimates throughout the range of observed PC1 values.

## DISCUSSION

### Survival

Understanding the factors that influence reintroduction success is critical for effective translocation and species recovery efforts. We evaluated the annual survival of stocked juvenile CRCT in relation to ex situ rearing strategies and habitat condition at the stocking locations. Overall, annual survival probabilities were low. The most prolific rearing treatment had 84% annual mortality when stocked in 2015 and 93% when stocked in 2016; additional treatments ranged from 94% to 98% annual mortality. In contrast, calculated or reported percentages of annual mortality of wild riverine CRCT populations in Willow Creek, Colorado; Little Muddy Creek, Colorado; and North Fork Little Snake River, Wyoming, were 43, 63, and 80%, respectively (Carlson and Rahel 2007). The high mortality rates in our study suggest deficient survival regardless of stocking and rearing manipulations.

However, variation in survival among the treatments suggests that a comprehensive approach to evaluating the success of CRCT reintroduction efforts will benefit future projects. We estimated maximum survival probability at 0.16 and 0.24 when considering the independent effect of

TABLE 2. Subset of top models from initial capture ($p$), recapture ($c$), and survival ($S$) modeling stages, with annual CRCT survival estimated using a robust design capture–recapture model with a Huggins estimator. The plus (+) signs denote additive parameters, and the asterisks (*) denote interactive parameters. "Session" refers to secondary sampling sessions, "time" refers to primary period (i.e., year), and "trt" refers to rearing treatment. The temporary emigration parameters ($\gamma_i''$ and $\gamma_i'$) were fixed to zero in all of the models. The complete model sets are available in the Supplementary Material: Tables D1 and D2.

| Candidate model | $K$ | AIC$_c$ | ΔAIC$_c$ | $w$ |
|---|---|---|---|---|
| **$p$ and $c$ stage** | | | | |
| $S_{(\text{time + trt})}$ $p_{(\text{UDA + session})}$ $c_{(\text{UDA + trt})}$ | 18 | 5,673.96 | 0.00 | 0.93 |
| $S_{(\text{time + trt})}$ $p_{(\text{UDA})}$ $c_{(\text{UDA + trt})}$ | 16 | 5,681.42 | 7.46 | 0.02 |
| $S_{(\text{time + trt})}$ $p_{(\text{session})}$ $c_{(\text{UDA + trt})}$ | 17 | 5,681.85 | 7.89 | 0.02 |
| $S_{(\text{time + trt})}$ $p_{(\text{UDA + trt})}$ $c_{(\text{UDA + trt})}$ | 21 | 5,682.50 | 8.54 | 0.01 |
| **Survival stage** | | | | |
| $S_{(\text{trt * PC1})}$ $p_{(\text{UDA + session})}$ $c_{(\text{UDA + trt})}$ | 23 | 5,524.06 | 0.00 | 0.90 |
| $S_{(\text{trt + PC1})}$ $p_{(\text{UDA + session})}$ $c_{(\text{UDA + trt})}$ | 18 | 5,529.14 | 5.08 | 0.07 |
| $S_{(\text{trt + PC1 + PC2})}$ $p_{(\text{UDA + session})}$ $c_{(\text{UDA + trt})}$ | 19 | 5,531.02 | 6.97 | 0.03 |
| $S_{(\text{PC1})}$ $p_{(\text{UDA + session})}$ $c_{(\text{UDA + trt})}$ | 13 | 5,561.80 | 37.74 | 0.00 |

TABLE 3. Initial capture ($p$) and recapture ($c$) probabilities from our top model. The values for $p$ varied as a function of secondary trapping session and $c$ as a function of treatment. Upstream drainage area exhibited a negative effect on both $p$ ($\beta_{\text{UDA}} = -0.02 \pm 0.006$) and $c$ ($\beta_{\text{UDA}} = -0.02 \pm 0.004$) probabilities. The subscripts note the year that each treatment was stocked.

| $p$ varies by | Probability | SE | CI (−) | CI (+) |
|---|---|---|---|---|
| Session 1 | 0.27 | 0.06 | 0.17 | 0.39 |
| Session 2 | 0.18 | 0.05 | 0.10 | 0.30 |
| Session 3 | 0.14 | 0.05 | 0.07 | 0.28 |
| $c$ varies by | | | | |
| $1D8_{'15}$ | 0.46 | 0.06 | 0.35 | 0.58 |
| $1D8_{'16}$ | 0.17 | 0.01 | 0.15 | 0.19 |
| $1D9_{'15}$ | 0.23 | 0.06 | 0.13 | 0.37 |
| $1D9_{'16}$ | 0.23 | 0.02 | 0.20 | 0.26 |
| $0S10_{'15}$ | 0.29 | 0.04 | 0.22 | 0.36 |
| $0S10_{'16}$ | 0.31 | 0.06 | 0.21 | 0.44 |

rearing treatment or receiving habitat characteristics, respectively. However, when we considered the interactive effect of both predictors, the maximum potential for survival reached 0.38, exhibiting over a 58% increase relative to the independent effects of either predictor. Failure to evaluate the potential interactions of rearing treatment and receiving habitat characteristics could lead to unnecessary repetition of stocking effort in future reintroduction projects.

The survival probability of CRCT from treatment 0S10 in 2015 was significantly greater than that for all of the other treatments. The 0S10 fish were age-0 at stocking and spent the least amount of time in an artificial rearing facility (4 months) compared with the other treatments (13–15 months). This provides limited support for the notion that restricting ex situ rearing exposure may increase survival, possibly by minimizing detrimental habituation to artificial hatchery conditions (Stringwell et al. 2014). The 0S10 fish were stocked latest in the year (October), so it is also possible that higher survival was because of less time spent in the wild or some other advantage to being stocked later in the year. Age-0 fish will need to survive longer to reach maturity, so the benefit of increased survival may be offset by the need to survive longer to age of first reproduction. In addition, caution should be taken in interpreting these results, as treatment 0S10 failed to produce significantly higher survival probabilities when stocked the following year (2016). In 2016, the fish were tagged and released at a smaller size due to year-to-year hatchery variation and the number of rejected tags, and posttagging mortality was also higher for 0S10 in 2016 (Table 1). Additional factors that this study was not designed to test (e.g., time-varying flow characteristics) may also be playing a role in differential survival between years.

Annual survival probability declined as PC1 values increased, suggesting some advantage to stocking CRCT in smaller headwater reaches. These results are consistent with those from previous research indicating that small streams, those measuring 1.5–2 m in bankfull channel width (Rosenfeld et al. 2002) and <5-m channel width (Rosenfeld et al. 2000), contribute disproportionally to rearing habitat for juvenile CRCT. The mechanisms driving these patterns are difficult to discern, although Rosenfeld et al. (2000) hypothesized that smaller, structurally complex streams may provide more edge habitat and more "hydrologically benign" rearing environments than large rivers. Our results support this because headwater sites with low PC1 values were also associated with increased pool cover (i.e., complexity) and decreased minimum and mean discharge while always maintaining sustainable flows. A lower degree of variation around higher mean flows throughout the main stem further suggests that fish that are stocked in those sites must combat higher sustained mean flows. The interactive effect between treatment and PC1 suggests that rearing treatment interacts with habitat characteristics of stocking locations to affect survival. The maximum estimated survival probability ($y$-intercepts, Figure 5) for treatment

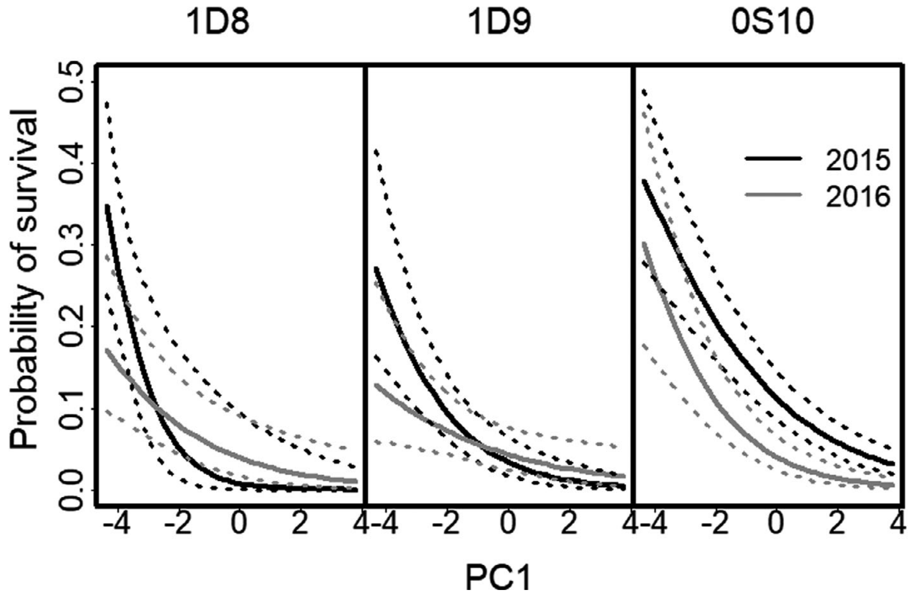


FIGURE 5. Interactive effect of treatment and PC1 on the annual survival probability of CRCT. The mean estimates (solid lines) and 95% confidence intervals (dashed lines) were derived from our top ranked robust design capture–recapture model with a Huggins estimator. Survival probabilities were estimated for fish that were stocked in 2015 (black lines) and 2016 (gray lines). The treatment codes that appear above each graph are explained in Table 1.

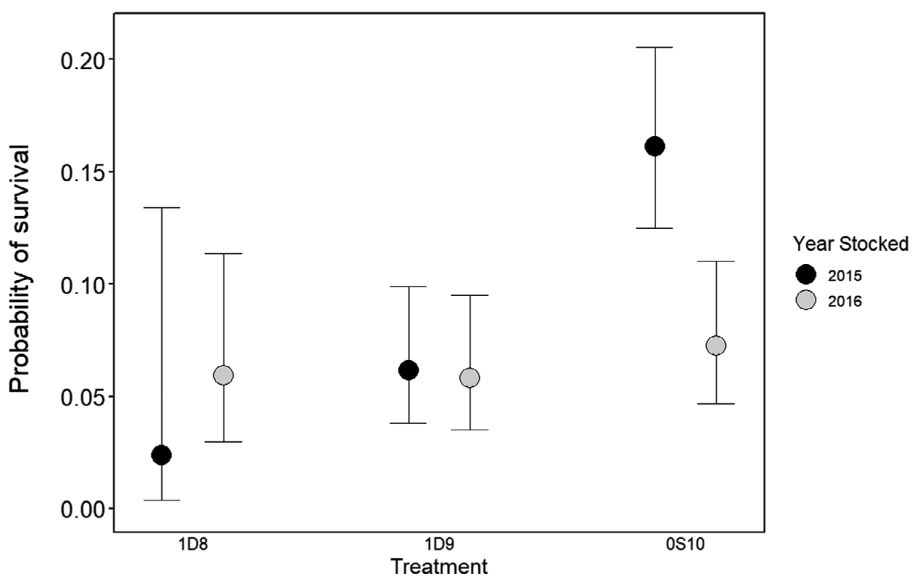


FIGURE 6. Annual survival probability for each estimable treatment stocked in 2015 and 2016. The mean estimates and 95% confidence intervals (error bars) were derived from our top ranked robust design capture–recapture model with a Huggins estimator. The treatment codes are explained in Table 1.

0S10 suggests that the benefits of limited ex situ rearing and small size may be exploited more effectively by introducing individuals to headwater stream segments where the selective mortality of maladaptive phenotypes could be reduced (e.g., decreased discharge relative to swimming ability; McDonald et al. 1998).

The mechanisms underlying low survival ultimately remain unclear. We did not explicitly examine stocking density, but the overall stocking numbers have been adjusted from originally high rates (2008–2010: 40,000–48,000 fish/year) to lower rates that should minimize density dependence (2011–2016: 14,000–18,000 fish/year;

Figure A). The progeny that were used for all of the treatments came from one source population in North Piney Lake, a relatively small water body that is connected to a single, second-order montane stream. This lentic population could be largely self-contained, leading to local adaptation and loss of genetic diversity through time (Carim et al. 2016). For instance, morphological differences that are associated with optimized swimming performance (Langerhans 2008; Haas et al. 2010; Franssen et al. 2013) and behavioral differences with respect to territoriality (Swain and Holtby 1989) may hinder the ability of individuals from a lentic source to establish in a lotic system. Adaptation to local conditions (e.g., temperature, water velocity) and decreased genetic heterozygosity may prove problematic when repopulating a lotic environment with a lentic brood source (Andrews et al. 2016).

Habitat availability and quality was another concern. Although LaBarge Creek supported Cutthroat Trout populations pretreatment, those fish may have been locally adapted to the thermal and environmental conditions specific to the drainage (Underwood et al. 2012). Although our top survival model excluded the effects of temperature, five of nine temperature-monitoring sites produced mean M30AT values that were within ranges that are associated with low to no growth and recruitment of juvenile CRCT (Harig and Fausch 2002; Bear et al. 2007; Coleman and Fausch 2007a, 2007b, as cited in Roberts et al. 2013). Also, lotic habitat that is provided via beaver impoundments was nonexistent in two of the tributaries that were surveyed due to beaver removal during the early phases of the reclamation effort to facilitate drainagewide chemical treatments. A lack of beaver recolonization could be limiting the availability of overwintering habitat, which is when it appears that most mortality is occurring (Kemp et al. 2012).

Predation is another plausible explanation for low survival. While there are no fish predators present, we observed American mink *Mustela vison* instream on three occasions and river otter *Lutra canadensis* on two and found five tags in riparian areas. Significant predation of trout by both species is well documented in streams systems (Lindstrom and Hubert 2004; Jacobsen 2005). Another concern could be lack of prey resources; a study on LaBarge Creek tributaries found some short-term negative effects on invertebrates when antimycin and rotenone were used in combination (Cerreto 2004). However, the treatment effects are generally short lived (Pham et al. 2018), more than 8 years have passed since treatment, and macroinvertebrate densities currently appear high throughout the drainage.

## Fish Movement

Emigration out of the study area did not appear to limit the reestablishment of CRCT. We were unable to maintain stationary PIT antennas year-round, yet we recovered only four tags below the barrier during supplemental sampling, suggesting that substantial emigration events did not occur while the antennas were not operational. Similar translocation monitoring programs conducted for Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* in the Cherry Creek drainage, Montana (90 km restored), reported that 90.9% of age-1 fish and 58.3% of age-2 fish remained within 1,000 m of their introduction site, with the farthest distance moved downstream being 6,185 m (Andrews et al. 2013). The downstream migration distance that is required to emigrate from LaBarge Creek drainage exceeds 6 km for all of the stocking locations that were employed. Documented within-drainage movement was also limited. Spring and Crystal creeks had the highest number of fish moving out of the tributary. As the smallest tributaries stocked, they received the highest average densities of fish so there may have been some density-dependent displacement, with smaller, poorly conditioned individuals moving downstream (Bujold et al. 2003; Westly et al. 2008). Nearly 75% of movements took place the year that individuals were stocked, suggesting that density-dependent movement is greater during initial competition immediately after stocking and that movement of 2015 stocked fish was likely underestimated.

## Model Considerations and Caveats

As is often the case with stocking studies, the study design was constrained by the availability of hatchery fish and management priorities. As a result, it was not possible to develop the ideal factorial design; instead, the treatments represented a combination of hatchery, size, and date of stocking that makes teasing apart the effects of any individual variable challenging. Thus, in addition to our efforts to achieve high spatial variation with respect to release sites for each treatment, future work should stock fish from each hatchery at different sizes and at different times to isolate which variables are important for survival and reintroduction success.

The large scale of the study (93 stream km) was great from a restoration standpoint but also meant that we were unable to sample the main stem in its entirety, which had implications for recapturing the fish. Our estimates represent apparent survival, as we cannot distinguish mortality from movement out of the sampled area. We do not know how much movement occurred within the main-stem LaBarge Creek, and high movement rates could result in underestimating survival probability. Similarly, variation in movement rates between treatments could affect the results. For example, an alternate interpretation for the higher survival for small fish could be that those fish are the least likely to move.

Our capture and recapture probabilities were negatively correlated with UDA, indicating lower detection of fish in the main stem than in tributaries. The inclusion of the individual, time-varying covariate UDA during capture ($p$) and recapture probability ($c$) modeling stages was critical in maintaining the integrity of survival estimates. Because we derived the UDA values for each capture location, we were explicitly able to account for irregularity in size among the survey reaches prior to modeling survival. Thus, we maintain that higher survival in the tributaries is a biologically driven phenomenon rather than a product of increased detection efficiency.

Given that UDA represented a similar headwater–main-stem gradient as PC1, future work may find it appealing to replace field-derived habitat measurements, which are time and labor intensive, with easily obtained geospatial variables. However, although UDA and PC1 were highly correlated (Pearson's correlation coefficient = 0.78), PC1 appeared in all of the top five models for survival (cumulative model weight = 1.0), while UDA did not appear in any of the top five models and only appeared in models with zero model weight. Thus, at least in our study, geospatial variables could not replace the more comprehensive field assessment of habitat conditions at stocking locations when predicting survival. We demonstrate that combining geospatial and field-derived variables can help more easily and appropriately model nuisance parameters such as capture and recapture probability while allocating time and effort to measuring variables that are hypothesized to influence parameters of interest such as survival.

## CONCLUSIONS

Despite 8 years of continuous stocking, CRCT density estimates remain substantially lower (0.2–1.5 fish/100 m) than historic salmonid density estimates based on removal numbers (~19 fish/100 m; included Brook Trout *Salvelinus fontinalis* and CRCT). The lack of older adult fish in recent electrofishing surveys suggests that poststocking survival may be one reason for the lack of persistence in these populations. The low annual survival estimates attained in this research support the assertion that survival remains suboptimal for reintroduction applications.

Manipulation of rearing history and stocking strategy using a single source population of CRCT produced some variation in annual survival probability, but it was limited. Given increased survival probabilities for the fish treatment exposed to ex situ rearing facilities for only 4 months, minimizing potential influences posed by artificial rearing may increase reintroduction success. One alternative that has proven successful in similar efforts involves translocating Cutthroat Trout embryos to instream remote-site incubators, virtually eliminating the potential for maladaptive traits to manifest ex situ (Andrews et al. 2013, 2016). We also found an interaction between rearing and stocking strategy, highlighting the importance of considering the life history stage of stocked individuals when identifying the stocking sites. The fish that were used in this study were juveniles, so annual survival increased via introduction to headwater refugia that likely provided a buffer to accumulating discharge in higher-order stream segments.

It may be that factors that we did not evaluate, such as habitat availability, resource availability, predators, and stocking density, are the limiting factors for poststocking survival of CRCT or that another life history stage is limiting population establishment and persistence. In addition, for this study only a single source of CRCT was available for reintroduction and it hailed from a lentic population so may not have been adapted to the environmental conditions in LaBarge Creek. Future studies investigating how local adaptation affects persistence in novel environments may provide critical information regarding the suitable selection of reintroduction stock when source populations are limited. Future reintroduction efforts may benefit from careful consideration of the genetic structure and thermal tolerance within potential source populations, identification of possible needs for admixture or mixed-source reintroduction stock, and evaluation of other factors that may be limiting establishment and persistence.

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.