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### Brown Trout Removal Effects on Short-Term Survival and Movement of *Myxobolus cerebralis*-Resistant Rainbow Trout

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ARTICLE

## Brown Trout Removal Effects on Short-Term Survival and Movement of *Myxobolus cerebralis*-Resistant Rainbow Trout

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### Abstract

Following establishment of *Myxobolus cerebralis* (the parasite responsible for salmonid whirling disease) in Colorado, populations of Rainbow Trout *Oncorhynchus mykiss* experienced significant declines, whereas Brown Trout *Salmo trutta* densities increased in many locations across the state, potentially influencing the success of *M. cerebralis*-resistant Rainbow Trout reintroductions. We examined the effects of Brown Trout removal on the short-term (3-month) survival and movement of two crosses of reintroduced, *M. cerebralis*-resistant Rainbow Trout in the Cache la Poudre River, Colorado. Radio frequency identification passive integrated transponder tags and antennas were used to track movements of wild Brown Trout and stocked Rainbow Trout in reaches where Brown Trout had or had not been removed. Multistate mark–recapture models were used to estimate tagged fish apparent survival and movement in these sections 3 months following Brown Trout removal. A cross between the German Rainbow Trout and Colorado River Rainbow Trout strains exhibited similar survival and movement probabilities in the reaches, suggesting that the presence of Brown Trout did not affect its survival or movement. However, a cross between the German Rainbow Trout and Harrison Lake Rainbow Trout exhibited less movement from the reach in which Brown Trout had been removed. Despite this, the overall short-term benefits of the removal were equivocal, suggesting that Brown Trout removal may not be beneficial for the reintroduction of Rainbow Trout. Additionally, the logistical constraints of conducting removals in large river systems are substantial and may not be a viable management option in many rivers.

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Following its establishment in Colorado, *Myxobolus cerebralis*, the parasite responsible for salmonid whirling disease, caused significant declines in wild populations of Rainbow Trout *Oncorhynchus mykiss* across the state. Brown Trout *Salmo trutta*, however, are more resistant to *M. cerebralis* than Rainbow Trout, having evolved with *M. cerebralis* in their

native, European home ranges (Hoffman 1970; Hedrick et al. 1999; Hedrick et al. 2003); as such they did not experience similar population level declines (Nehring and Thompson 2001; Nehring 2006). Consequently, Brown Trout densities increased in many of Colorado's rivers following the loss of Rainbow Trout populations (Nehring and Thompson 2001).

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Similar Brown Trout increases were observed in several drainages in Montana following *M. cerebralis*-induced Rainbow Trout declines (Baldwin et al. 1998; Granath et al. 2007).

Competition with and predation by Brown Trout can cause significant declines in sympatric salmonid populations, including Brook Trout *Salvelinus fontinalis* (Fausch and White 1981; Alexander 1977), Cutthroat Trout *Oncorhynchus clarkii* (Wang and White 1994), and Rainbow Trout populations (Gatz et al. 1987). Competition with Brown Trout results in exclusion of Rainbow Trout from preferred feeding and resting habitats, possibly causing population-level effects (Gatz et al. 1987). High densities of large Brown Trout exert heavy predation pressure on stocked Rainbow Trout juveniles (75 mm TL; Nehring 2006) as well as compete with subcatchable ( $\leq 150$  mm TL) and catchable-sized ( $\geq 250$  mm TL) *M. cerebralis*-resistant Rainbow Trout being reintroduced to Colorado waters.

Brown Trout switch to piscivory at approximately age 3 ( $> 175$  mm TL; Jonsson et al. 1999), when energy intake and growth tend to increase markedly (Elliott and Hurley 2000). Piscivorous Brown Trout can significantly alter both sympatric salmonid and other prey species population structure and dynamics. Large Brown Trout are known to consume considerable numbers of small trout and are a significant source of fry ( $< 75$  mm TL) and fingerling mortality in sympatric salmonid populations (Alexander 1977). In addition, Brown Trout prey largely on other salmonid species rather than consuming juveniles of their own species, and the number consumed increases with an increase in Brown Trout length (Jensen et al. 2006). Jensen et al. (2006) calculated that a Brown Trout population (8,445 individuals  $> 250$  mm TL) consumed about 1.5 million Vendace *Coregonus albula* and 400,000 Lake Whitefish *C. clupeaformis* annually, illustrating the negative effects that large, piscivorous Brown Trout can have on other fish populations.

Control and eradication of Brown Trout are potential management options for reducing competition and predation effects and increasing the survival of other salmonid and prey fish species (Gatz et al. 1987). Considerable removal efforts may be needed to attain a desired effect on target populations. For example, removal of 66% of the Brown Trout population in the Au Sable River in Michigan did not result in population or size-at-age increases in the sympatric Brook Trout population (Shetter and Alexander 1970). Predatory Brown Trout numbers may therefore need to be reduced by considerably more than 60% to attain a significant increase in survival or change in other population characteristics of target species (Alexander 1977).

In our study, Brown Trout were removed from a 1.0-km reach of the Cache la Poudre River, Colorado, and two crosses of *M. cerebralis*-resistant Rainbow Trout were stocked into this reach and a 1.3-km control reach where Brown Trout were not removed. We used radio frequency identification of passive integrated transponder (PIT) tags and antennas to estimate survival and movements of wild Brown Trout and

stocked Rainbow Trout in these two reaches. The objectives of this study were to (1) determine what factors influence estimates of short-term apparent survival and movement probabilities for Brown Trout and Rainbow Trout among reaches, (2) determine if Brown Trout removal increased the short-term survival and retention of either of the Rainbow Trout crosses, and (3) estimate changes in wild Brown Trout and stocked Rainbow Trout population abundances in both reaches.

## METHODS

*Site description.*—The Cache la Poudre River is a high-gradient freestone river that originates in Rocky Mountain National Park and flows north and east until joining the South Platte River on the eastern plains of Colorado (Sipher and Bergersen 2005). Maximum summer temperatures range from 5°C to 12°C annually and rarely exceed 13°C (Nehring and Thompson 2001). Rainbow Trout and Brown Trout are the principle game fish, but Brook Trout, Cutthroat Trout, and Mountain Whitefish *Prosopium williamsoni* are also present in low numbers (Klein 1963; Allen and Bergersen 2002).

*Myxobolus cerebralis* was first detected in the Cache la Poudre River drainage in 1988. Prior to the establishment of *M. cerebralis*, age-1 and older Rainbow Trout were found in higher densities (170 fish/ha) than age-1 and older Brown Trout (103 fish/ha; Nehring and Thompson 2001), or a historical average ratio of 60 Rainbow Trout to 40 Brown Trout (Klein 1963). By 1995, severe declines were experienced by the Rainbow Trout population, and no age-1 and older Rainbow Trout were detected in population estimates. Brown Trout, however, did not suffer significant population level declines (Nehring and Thompson 2001), and Brown Trout biomass compensated for the loss of Rainbow Trout to some degree (Allen and Bergersen 2002).

Two reaches of the Cache la Poudre River were selected for this experiment, a control reach (no removal) and a removal reach (Brown Trout removal). The 1.3-km control reach was located just downstream of the town of Rustic, Colorado, in an area known as Indian Meadows, and the 1.0-km removal reach was located 8 km upstream of the control reach in an area known as Black Hollow (Figure 1). Both study reaches were located in special regulation catch-and-release sections to prevent angler removal of PIT-tagged fish. All Brown Trout captured in the removal reach were relocated approximately 24.1 km downstream, below a high-velocity section of the river known as the Narrows (Figure 1). Fish were relocated rather than sacrificed to maintain public support for the experiment.

*Rainbow Trout crosses.*—Two crosses of *M. cerebralis*-resistant Rainbow Trout were evaluated in this study: a cross between the German Rainbow Trout and Colorado River Rainbow Trout (GR  $\times$  CRR) and a cross between the German Rainbow Trout and Harrison Lake Rainbow Trout (GR  $\times$  HL) strains. The German Rainbow Trout is a hatchery-derived strain that was exposed to *M. cerebralis* over multiple

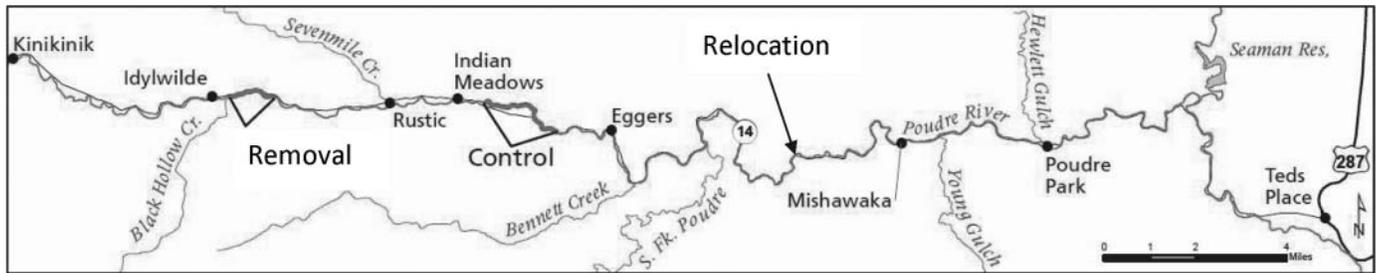


FIGURE 1. Location of the control, removal, and relocation reaches within the Cache la Poudre River, Colorado, where effects of Brown Trout removal were examined on two crosses of *M. cerebralis*-resistant Rainbow Trout: (1) German Rainbow Trout by Colorado River Rainbow Trout (GR  $\times$  CRR) and German Rainbow Trout by Harrison Lake Rainbow Trout (GR  $\times$  HL).

generations in Germany (Hedrick et al. 2003), developing “resistance” to *M. cerebralis*. Although German Rainbow Trout can be infected with *M. cerebralis*, parasite burdens are usually low (Hedrick et al. 2003; Schisler et al. 2006; Fetherman et al. 2012), and they can survive and reproduce in the presence of *M. cerebralis*. While domestication facilitated pathogen resistance, the strain’s viability in the wild was uncertain (Schisler et al. 2006), which led to its experimental crossing with the CRR (Schisler et al. 2006; Fetherman et al. 2011; Fetherman et al. 2012) and HL (Schisler 2006) strains.

Colorado River Rainbow Trout were widely stocked and used to establish many naturally reproducing Rainbow Trout populations in Colorado prior to the establishment of *M. cerebralis* (Walker and Nehring 1995). However, the Colorado River Rainbow Trout exhibit high susceptibility to infection by *M. cerebralis* (Ryce et al. 2001; Sipher and Bergersen 2005; Schisler et al. 2006; Fetherman et al. 2012) and experienced widespread population declines following its establishment in Colorado (Nehring and Thompson 2001). The GR  $\times$  CRR cross has been experimentally introduced to other rivers within the state but has exhibited low apparent survival in high-density, Brown Trout-predominated systems (Fetherman et al. 2014). Brown Trout removal was therefore evaluated as a means to increase the survival and retention of the GR  $\times$  CRR cross.

Harrison Lake Rainbow Trout (origin: Harrison Lake, Montana) exhibit enhanced resistance to *M. cerebralis* relative to other Rainbow Trout strains, which could be related to ancestry (Vincent 2002; Wagner et al. 2006). This HL strain has also exhibited rapid development of resistance to *M. cerebralis* through natural selection (Miller and Vincent 2008). Resistance was increased significantly when HL fish were crossed with GR fish (Schisler 2006). However, due to its history as a lake strain (Wagner et al. 2006), the survival and retention of the GR  $\times$  HL cross following river introductions was unknown and was therefore evaluated in this experiment.

**Fish marking procedures.**—The 4,000 Rainbow Trout we tested, 2,000 of each cross, were measured (mm), weighed (g), and tagged with a half-duplex (HDX) passive integrated transponder (PIT) tag (32  $\times$  3.85 mm) inserted posterior of the pectoral fin through the midventral body wall into the peritoneal cavity via a hypodermic needle (Prentice et al. 1990;

Acolas et al. 2007). After tagging, fish were held 1.5 months prior to being stocked. Crosses were differentially fin clipped so that identification would be possible during population estimates in the event of tag loss. During tagging, GR  $\times$  CRR and GR  $\times$  HL fish were randomly separated into two groups of 1,000 fish each (known tag numbers in each group) designated for introduction to either the control or removal reaches. We evaluated tag retention and tag-related mortality 1 month post-tagging. Tag retention was calculated as the proportion of 100 indiscriminately selected fish from each group of 1,000 that retained their tags, as evaluated using a handheld portable PIT tag reader. Mortality was calculated based on the number of dead fish removed from the raceways by Colorado Parks and Wildlife (CPW) staff.

To evaluate whether there were differences in length or weight among the GR  $\times$  CRR and GR  $\times$  HL crosses stocked into the reaches, we used a generalized linear model (GLM) implemented in SAS ProcGLM (SAS Institute, 2010). We considered an intercept-only model, as well as models that included effects of cross only, reach only, and additive and interactive effects between cross and reach. Models were ranked using Akaike’s Information Criterion corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). Model weights and  $\Delta AIC_c$  were used to determine support for each model, and parameter estimates were reported from the candidate model with the lowest  $AIC_c$  value (Burnham and Anderson 2002).

A total of 676 Brown Trout were captured and PIT-tagged 1 week prior to the introduction of Rainbow Trout, 270 within the 1.3-km control reach plus 222 upstream and 184 downstream of the reach. Three passes were made on consecutive days using two raft-mounted electrofishing units. All fish encountered on the first pass were PIT-tagged, measured, weighed, and released in the same area of capture. On subsequent passes, untagged fish were similarly tagged, measured, and weighed, and tag numbers from previously tagged fish were recorded. By PIT-tagging fish upstream, within, and downstream of the control reach we were able to estimate the survival and movement probabilities of Brown Trout following Rainbow Trout introduction.

**Brown Trout removal.**—Brown Trout removal occurred August 16–18, 2010, 1 week following PIT tagging operations

in the control reach and antenna installation in both reaches. Prior to the removal, block fences constructed of chicken wire fencing attached to T-bar posts were erected across the river at the upstream and downstream ends of the reach to prevent fish from moving out of (or into) the section during the removal. Fences were monitored continuously to prevent build-up of debris, and fencing did not fail during the removal. The removal was accomplished using 14 Smith-Root LR-24 backpack electrofishing units; four raft-mounted, fixed-boom electrofishing units; and one three-electrode cat-raft. Over 100 CPW biologists, researchers, and volunteers assisted with the removal. Backpack and cat-raft crews formed one continuous line across the width of the river and worked upstream from the bottom of the reach, completing five passes over the 3-d removal, one pass on the first day, and two passes on each of the subsequent days. Raft electrofishing crews made several passes daily. Fish collected by the raft electrofishing crews were combined with fish collected at the same time by backpack and cat-raft crews.

Brown Trout removed from the reach were measured and weighed, placed in well oxygenated tanks on hatchery trucks, and transported downstream to the relocation section at the end of each day. All other species encountered during the removal, including 26 Rainbow Trout, 5 Longnose Sucker *Catostomus catostomus*, and 1 White Sucker *Catostomus commersonii*, were returned to the river below the downstream block fence.

Brown Trout located in the 0.8-km sections upstream ( $N = 182$ ) and downstream ( $N = 216$ ) of the removal reach were captured and PIT-tagged using the same methods described above and returned to the section from which they had been caught. By PIT tagging Brown Trout upstream and downstream of the reach we were able to monitor movement back into the reach following the removal.

We estimated Brown Trout abundance upstream, within, and downstream of the control reach using the Huggins closed capture–recapture estimator (Huggins 1989, 1991) in Program MARK (White and Burnham 1999). We considered models where initial capture probability ( $p$ ) and recapture probability ( $c$ ) were different, as well as other models where these two parameters were set equal. In addition, pass and fish length were explored as covariates that might have influenced  $p$  or  $c$  (20 models). We used the same estimator to estimate the initial number of Brown Trout and wild Rainbow Trout present in the removal reach, but  $c$  was fixed to zero because removed individuals were not available for recapture (Hense et al. 2010; Saunders et al. 2011). In this analysis, captured fish were classified into four groups, and used as a categorical covariate in the analysis: (1) adult Brown Trout ( $>150$  mm), (2) fry and juvenile Brown Trout ( $\leq 150$  mm), (3) adult Rainbow Trout ( $>150$  mm), and (4) fry and juvenile Rainbow Trout ( $\leq 150$  mm). We considered models where  $p$  was constant or varied by group, pass, fish length, and all additive combinations (eight models). Models were ranked using  $AIC_c$  and reported as

model-averaged estimates of abundance and associated unconditional standard errors (Burnham and Anderson 2002).

*Rainbow Trout introduction.*—Rainbow Trout were introduced to both reaches the day following Brown Trout removal. The control reach could only be accessed by raft, so Rainbow Trout were exchanged from the hatchery truck into coolers containing a mix of hatchery and river water, and loaded onto rafts about 0.8 km upstream of the reach. Stocking commenced upon entering the reach, and Rainbow Trout were evenly distributed throughout the reach. The removal reach allowed easy access for stocking by foot. Rainbow Trout were stocked about 0.5 km downstream of the upper end of the reach, in the middle of the reach, and at the lower end of the reach. At each location, fish were evenly distributed throughout the reach using buckets to disperse releases. Block fences were removed following Rainbow Trout introduction.

*PIT tag antennas.*—We deployed radio frequency identification HDX PIT tag antennas at the upstream and downstream ends of both reaches prior to Brown Trout removal. Pass-over antenna loops were constructed of eight-gauge, multistrand copper speaker wire anchored to the substrate with duckbill anchors. The speaker wire was connected to a tuner box, used to tune the antenna for optimal detection distance, and tuner boxes were connected to a reader using twin-ax cable. Antenna loops were paired at all locations to determine directionality of movement, and attached to a multiplexer reader to prevent proximity detection errors (Aymes and Rives 2009). Readers were powered by two 12-V marine deep-cycle batteries (120 amp-hours) connected in parallel.

Antennas, which spanned the width of the river, ranged from 18.3 to 24.5 m in length and averaged 0.9 m in width. Optimal antenna placement was chosen based on laboratory detection experiments that showed that  $p$  was  $\geq 0.89$  when fish passed within 0.6 vertical m of the antenna, and when velocity did not exceed 0.50 m/s. Antennas were placed in glides that satisfied these conditions. Average depth at the antennas during the highest discharge period did not exceed 0.4 m. To reduce the possibility of tag collision (Axel et al. 2005; O'Donnell et al. 2010), antennas were placed such that velocity refuges were not contained within or between loops.

Antennas were run continuously from August 15 to November 3, 2010, and efficiency ( $E$ ; Zydlewski et al. 2006) was monitored on a weekly basis using the stick-test method (Nunnallee et al. 1998; Compton et al. 2008). Velocity measurements were collected at the same time and used to calculate discharge ( $m^3/s$ ), included as a covariate affecting probability of movement in the multistate capture–recapture analyses.

*Multistate capture–recapture models.*—Multistate capture–recapture models provide a useful approach to estimating animal movement and survival probabilities (Hestbeck et al. 1991; Brownie et al. 1993; Lebreton and Pradel 2002) and have recently been applied to complex studies of fish movement and migration patterns based on highly structured tagging data (Buchanan and Skalski 2010; Horton et al. 2011;

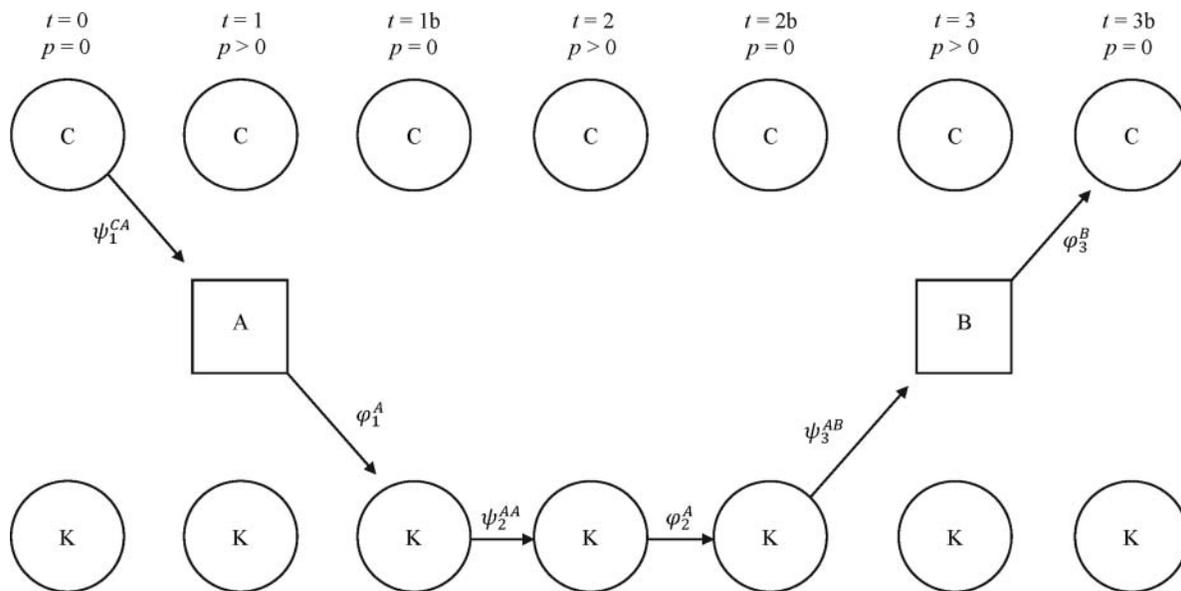


FIGURE 2. Example of the multistate model used to estimate movement ( $\psi$ ), survival ( $\phi$ ), and detection probability ( $p$ ) for a fish with the 3-week encounter history of CA000B0, i.e., an individual fish released in the control reach (release state C) at time 0. Fish were not physically recaptured in release states (circles), thus  $p$  for these states is zero. In week 1, the fish was recaptured (squares) making a downstream movement past the lower control antenna station (state A). Therefore, the transition probability ( $\psi^{CA}_1$ ) was estimated between periods 0 and 1, and apparent survival ( $\phi^A_1$ ) was estimated following the transition between periods 1 and 1b. In week 2, the fish remained downstream, and the probability of retention ( $\psi^{AA}_2$ ) and apparent survival ( $\phi^A_2$ ) were estimated. In week 3, the fish was observed making an upstream movement (state B). Therefore,  $\psi^{AB}_3$  was estimated between periods 2b and 3, and  $\phi^B_3$  was estimated between periods 3 and 3b. At periods 1, 2, and 3,  $p$  was fixed to the adjusted efficiency for the lower control antenna station (Table 1).

Frank et al. 2012). These models allow estimation of apparent survival ( $\phi$ ), detection ( $p$ ), and movement probabilities ( $\psi$ ) between and among states (Lebreton and Pradel 2002), including spatial or geographical location and physiological status (Buchanan and Skalski 2010). In our study, states were defined by spatial location (reaches) and transition location (directional movement at antenna stations). Primary assumptions are that (1) marks are not lost, (2) individuals act independently, and (3) all marked individuals assigned to a state have the same probabilities of survival, movement, and capture (Hestbeck 1995).

Traditional multistate models, using physical recaptures, estimate a single parameter describing the probability that an individual in state  $r$  at time  $t$  survives and is in state  $s$  at time  $t+1$ . To separate the two processes (survival and movement), an assumption is made that movement occurs at the end of the interval between  $t$  and  $t+1$ , and thus, survival is a function of the departure state. This assumption allows estimation of two parameters, apparent survival ( $\phi^r$ ) and movement ( $\psi^{rs}$ ; Brownie et al. 1993). However, if this assumption is inconsistent with the study system, biases can result (Hestbeck 1995).

In our case, we used antenna detections as recaptures when estimating the parameters of the multistate models (O'Donnell et al. 2010). Fish were recaptured at stationary antenna stations as they moved between states, thus survival prior to movement was known (1.0) and survival following movement was unknown. This reversal of the survival and movement process requires inclusion of an additional "dummy" time interval associated with each sampling interval. Therefore, a

paired record was included in the encounter history, the first value representing observed movement (movement state or 0 [zero] for lack of movement). The second value was a dummy variable (always 0) that allowed us to estimate movement ( $\psi$ ) before apparent survival ( $\phi$ ; Figure 2).

Encounter histories for each tagged individual began with a release state, which appeared only once in the history. Rainbow Trout had two release states, whereas Brown Trout had five release states depending on their location at tagging (Figure 3). The remainder of the encounter history consisted of unique movement states used to represent both direction and location of the detected movement (Figures 2, 3). Movement occurred if two conditions were met: (1) the fish was detected by both antennas within the array (i.e., directionality of movement was known), and (2) there was no return movement within the same week (i.e., a fish did not begin and end the week in the same location). We assumed that if a tag was detected at an antenna station, the tag was in the fish that was originally tagged and that the fish was alive. Lack of movement was indicated by a 0 for two successive entries. For example, the 3-week encounter history CA000B0 represents a fish that was initially released in the control reach (state C), was detected moving downstream in week 1 (state A + dummy variable A0), remained downstream in week 2 (not detected + dummy variable 00), and was detected moving back upstream into the control reach in week 3 (state B + dummy variable B0; Figure 2).

Multistate models were constructed to estimate weekly apparent survival ( $\phi$ ) and movement ( $\psi$ ) probabilities for

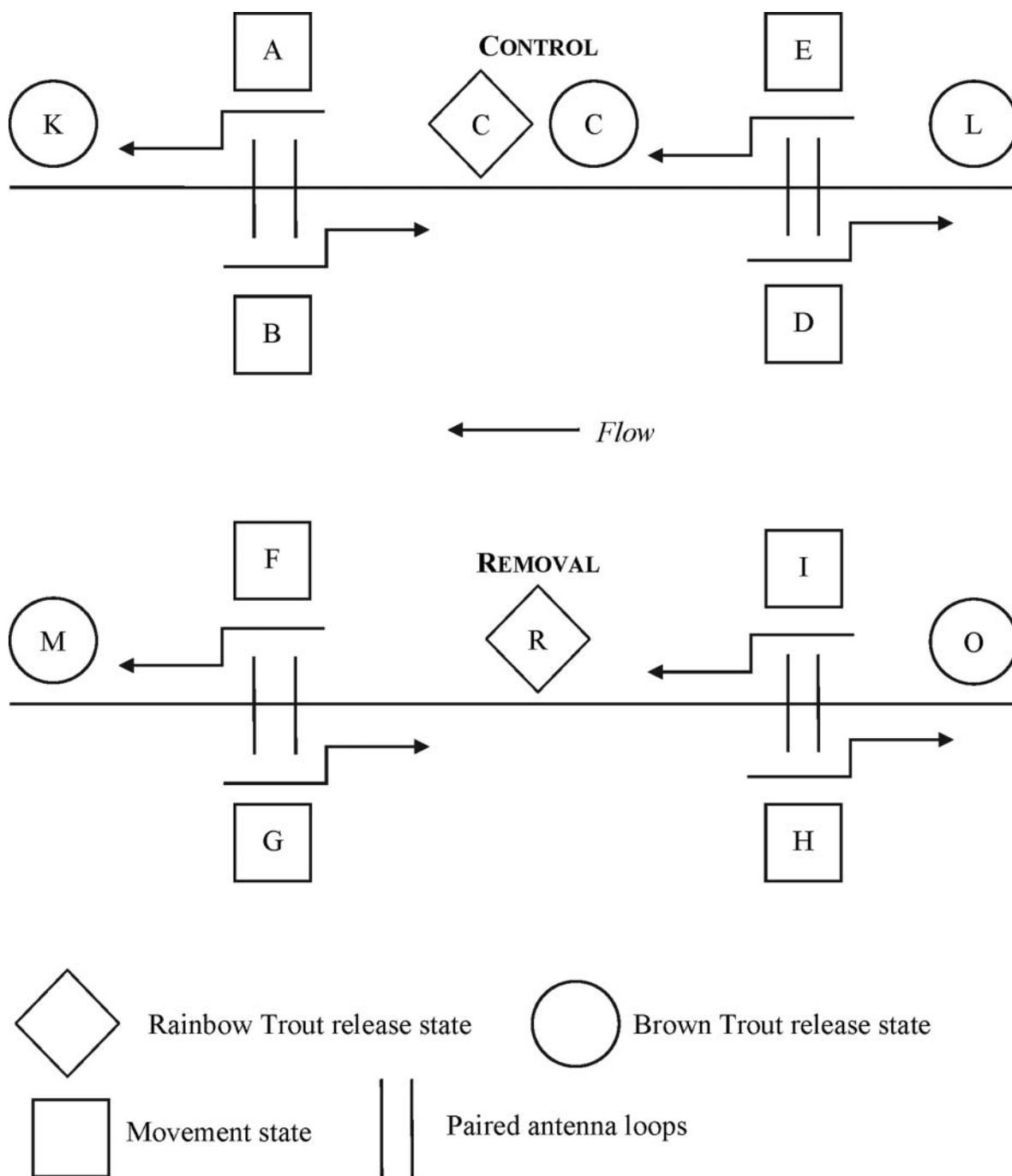


FIGURE 3. Release states for Rainbow Trout (GR × CRR and GR × HL; as explained in Figure 1) and Brown Trout, and movement states used in the multi-state models estimating weekly apparent survival ( $\varphi$ ) and movement ( $\psi$ ) probabilities for PIT-tagged (passive integrated transponder tags) fish in the control and removal reaches of the Cache la Poudre River, Colorado. Letters represent unique release states or movement states, as based on directionality of movement.

Brown Trout and Rainbow Trout in both reaches. Three model sets were used to separately estimate apparent survival and movement for Brown Trout and the GR × CRR and GR × HL crosses. Multistate models for Brown Trout consisted of 13 states: 5 release states and 8 movement states. Rainbow Trout multistate models consisted of 10 states: 2 release states and 8 movement states. The eight movement states remained the

same for both species, representing directional movement obtained via detections at each antenna location (Figure 3).

We estimated state-specific movement ( $\psi$ ) for each weekly time interval. Because of the distance between the study reaches, there was little movement between reaches (only four Brown Trout and two Rainbow Trout made movements between reaches). Therefore, all movements between reaches

TABLE 1. Antenna efficiencies for radio frequency identification of passive integrated transponder tags ( $E$ ; the probability of being detected at both antennas within an array) in the Cache la Poudre River, Colorado, as estimated on a weekly basis at each antenna location. Efficiencies were used to fix state-specific detection probability ( $p = E$ ) per week in the multistate capture–recapture analyses of tagged Rainbow and Brown Trout.

Week	Lower control	Upper control	Lower removal	Upper removal
Aug 19–Aug 26	0.91	0.54	0.73	0.77
Aug 27–Sep 2	0.90	0.65	0.88	0.88
Sep 3–Sep 9	0.71	0.29	0.66	0.76
Sep 10–Sep 16	0.85	0.38	0.78	0.82
Sep 17–Sep 23	0.91	0.44	0.91	0.82
Sep 24–Sep 30	0.96	0.67	1.00	0.89
Oct 1–Oct 7	0.92	0.54	0.96	0.94
Oct 8–Oct 14	0.90	0.63	0.91	0.89
Oct 15–Oct 21	0.94	0.60	0.96	0.88
Oct 22–Oct 28	0.92	0.58	0.93	0.90
Oct 29–Nov 3	0.92	0.58	0.93	0.90
Average	0.89	0.54	0.88	0.86

(e.g., movement from state L to state G; Figure 3) were fixed to zero. All other movements were considered estimable. In all three model sets,  $p$  for all release states was fixed to zero because individuals were never recaptured within a release state. Detection probabilities for each movement state were fixed to the antenna efficiencies measured weekly at each antenna array (Table 1).

Initial movement probabilities ( $\psi_I$ ) represented the probability that a fish moved from their release state. For Rainbow Trout,  $\psi_I$  values were compared between reaches and among the two crosses. We expected that Rainbow Trout released in the removal reach might exhibit lower movement out of the reach than the control and that the GR  $\times$  HL fish might be more likely to move than GR  $\times$  CRR fish. Likewise, we compared  $\psi_I$  for Brown Trout among sections to determine whether movement into the removal reach was higher than into the control reach. Subsequent or secondary movement probabilities ( $\psi_S$ ) were estimated via fish that moved from their original release state. This allowed us to differentiate  $\psi_I$  of fish during the first 2 weeks that might be elevated as a result of capture, marking, or introduction, from subsequent  $\psi_I$  and  $\psi_S$  of fish after they had acclimated. Note that  $\psi_S$  could not be estimated during the first week because movement from the release state ( $\psi_I$ ) was required for secondary movements to be observed.

Brown Trout and the GR  $\times$  CRR and GR  $\times$  HL model sets included apparent survival ( $\phi$ ) structures that were constant across time and states (null structure), varied by section (upstream, within, or downstream of the reaches), fish length (size-specific survival related to competition), or fish weight (size-specific survival associated with PIT tag size in relation

to fish size). Fish length and weight were determined at the time of release and included as individual covariates. All additive combinations were included in the model set, but length and weight were never included in the same model because they were correlated. Models also included variation in movement probability ( $\psi$ ) structures, including those where  $\psi$  was constant across time and states (null structure); varied by state, discharge (categorical covariate), fish length (size-specific movement related to competition); or varied within the first 2 weeks (i.e., state-specific  $\psi_{1,2} \neq \psi_{3-11}$ ). The Brown Trout model set also included models with an interaction between state and spawning season to test whether  $\psi$  varied during the prespawn (August 15 to September 3) versus spawning (September 24 to November 3) period. Similar to survival, all additive combinations were included in the model sets.

We fit all models using Program MARK and used model selection procedures to determine relative support for each candidate model. We report  $\Delta AIC_c$  and model weights for supported models (Burnham and Anderson 2002). Model-averaged estimates and unconditional 95% confidence intervals (CIs) were used to incorporate model selection uncertainty in the parameter estimates of  $\phi$  and  $\psi$ .

*Population abundance estimation.*—Population estimates were conducted in two shorter segments in each reach in late October 2010. Abundance estimation segments averaged 124 m in length and 17 m in width, and stream features, such as high-velocity riffles on the upstream end of the segments, were used to restrict fish movement during data collection. Three consecutive removal passes were made through each section using a four-electrode bank electrofishing unit. All fish captured were measured, weighed, scanned for PIT tag, and all Rainbow Trout were examined for fin clips to identify any GR  $\times$  CRR and GR  $\times$  HL fish that had lost their tags.

Abundance estimates for Brown Trout and Rainbow Trout in both reaches were obtained using a Huggins closed-capture recapture estimator. Brown Trout and GR  $\times$  CRR and GR  $\times$  HL crosses were included as groups in the same analysis. Models included various structures of  $p$ , including those in which  $p$  was constant, or varied by group, pass, fish length, and all additive combinations therein. Models were ranked using  $AIC_c$  and model-averaged estimates of abundance and unconditional standard errors were reported.

## RESULTS

### Fish Marking

Model selection results for differences in Rainbow Trout average total length indicated that the model including an interaction between cross and reach was most supported by the data ( $w_i = 0.99$ ; Table 2). In both reaches the GR  $\times$  CRR fish were longer than the GR  $\times$  HL fish, but the difference was slightly larger in the control reach, where GR  $\times$  CRR = 199.5 mm (SE = 0.8) and GR  $\times$  HL = 156.9 mm (SE = 0.8),

TABLE 2. Model selection results for differences in Rainbow Trout length and weight at stocking in the Cache la Poudre River, Colorado, in August 2010. The maximized log-likelihood ( $\log(L)$ ), the number of parameters ( $K$ ) in each model, and the small sample size-corrected AIC values ( $AIC_c$ ) are shown. Models are ranked within the length or weight model sets by their  $AIC_c$  differences ( $\Delta AIC_c$ ) relative to the best model in the set, and Akaike weights ( $w_i$ ) quantify the probability that a particular model is the best model in the set, given the data and the model set.

Model	$R^2$	$\log(L)$	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
<b>Length</b>						
Cross $\times$ reach	0.58	-11,181.40	4	22,372.86	0.00	0.99
Cross + reach	0.58	-11,190.30	3	22,387.80	14.94	0.01
Cross	0.58	-11,194.20	2	22,393.04	20.18	0.00
Reach	0.00	-12,895.50	2	25,795.59	3,422.73	0.00
Intercept only	0.00	-12,897.10	1	25,796.37	3,423.51	0.00
<b>Weight</b>						
Cross $\times$ reach	0.57	-12,032.40	4	24,074.88	0.00	0.99
Cross + reach	0.57	-12,039.30	3	24,085.88	11.00	0.01
Cross	0.57	-12,052.00	2	24,108.65	33.77	0.00
Reach	0.00	-13,706.10	2	27,416.84	3,341.96	0.00
Intercept only	0.00	-13,711.50	1	27,425.12	3,350.24	0.00

than in the removal reach, where  $GR \times CRR = 195.6$  mm ( $SE = 0.8$ ) and  $GR \times HL = 157.7$  mm ( $SE = 0.5$ ). Similarly, the same interaction model was well-supported when fitting our Rainbow Trout weight data ( $w_i = 0.99$ ; Table 2). Again,  $GR \times CRR$ s in both reaches were heavier than the  $GR \times HL$ s, but the differences were slightly larger in the control reach ( $GR \times CRR = 92.8$  g [ $SE = 1.0$ ] and  $GR \times HL = 41.2$  g [ $SE = 1.0$ ]) than in the removal reach ( $GR \times CRR = 86.8$  g [ $SE = 1.0$ ];  $GR \times HL = 40.3$  g [ $SE = 0.7$ ]). Differences in length and weight within a cross were negligible, suggesting that apparent survival and movement differences between the reaches within a cross were not due to differences in fish size.

Tagging mortality was 2.95% (59 mortalities) for  $GR \times CRR$  and 0.55% (11 mortalities) for the  $GR \times HL$ . The PIT tags ( $32 \times 3.85$  mm, 0.8 g) were 0.9% of the average  $GR \times CRR$  weight and 2.0% for  $GR \times HL$  average weight; it is unlikely that mortality was associated with PIT tag weight (Zale et al. 2005). Estimated tag retention was 98.5% for the  $GR \times CRR$  and 99% for the  $GR \times HL$ , which was similar to that observed in other studies (Roussel et al. 2000; Zydlewski et al. 2001; Compton et al. 2008). Therefore, differences in apparent survival and movement were not due to differential tag loss.

Model-averaged abundance estimates indicated that 1,028 ( $SE = 387$ ) Brown Trout  $\geq 120$  mm TL were present upstream of the control reach, and 1,354 ( $SE = 784$ ) were present downstream of the reach. Therefore, approximately 21% and 13% of the Brown Trout population was tagged in these two sections, respectively. Within the control reach, estimates indicated that 1,679 ( $SE = 451$ ) Brown Trout were present, and approximately 16% were tagged. Brown Trout tagged in the control reach averaged 275 mm TL ( $SE = 10$ ) and 221 g ( $SE = 5$ ). By comparison, Brown Trout upstream and downstream of the removal reach averaged 270 mm TL ( $SE = 12$ ) and 203 g ( $SE = 21$ ).

### Brown Trout Removal

A total of 1,399 Brown Trout were removed from the removal reach, 726 on the first day, 429 on the second day, and 263 on the third day. Model-averaged abundance estimates indicated that 1,975 ( $SE = 403$ ) Brown Trout were present in the reach prior to the removal; therefore, 71% of the population was removed. Of the estimated 834 ( $SE = 49$ ) adult Brown Trout, 744 were removed, equating to about 89% of the adult population. In contrast, 655 of the estimated 1,141 ( $SE = 354$ ) fry and juvenile Brown Trout were removed, equating to 57% of the fry and juvenile population. Fewer wild Rainbow Trout were estimated to be present in the removal reach, 26 ( $SE = 2$ ) adults and 4 ( $SE = 2$ ) fry and juveniles being present prior to the removal.

### Antenna Performance

All antenna stations were fully functional during our study. Antenna efficiencies were comparable to those in other studies (Zydlewski et al. 2006; Compton et al. 2008), ranging from 0.54 to 0.89 (Table 1).

### Rainbow Trout Apparent Survival

Rainbow Trout apparent survival was affected by section, fish length, and to a lesser extent, fish weight (Table 3). Apparent survival for both the  $GR \times CRR$  and  $GR \times HL$  crosses was most affected by section, which appeared in all supported models within both model sets. The  $GR \times CRR$ s did not exhibit differences in apparent survival between the reaches, whereas apparent survival was higher in the control reach than in the removal reach for the  $GR \times HL$ s (Figure 4). Comparing longitudinally for both crosses, apparent survival was higher within the reaches than in the sections upstream or

TABLE 3. Model selection results for multistate models fit to stocked Rainbow Trout data from the Cache la Poudre River, Colorado. The candidate model sets included over 150 models with various structures for apparent survival ( $\varphi$ ) and movement ( $\psi$ ). Models for which  $AIC_c$  weights were nonzero ( $w_i > 0$ ) are shown for both the GR  $\times$  CRR and GR  $\times$  HL crosses (see Figure 1). Models are ranked within the GR  $\times$  CRR or GR  $\times$  HL model sets by  $\Delta AIC_c$ , the  $AIC_c$  value of the model relative to the best model in the set, and Akaike weights ( $w_i$ ), representing the probability that the model is the best model, given the data and the model set. Also reported are the  $\log(L)$ , the number of parameters ( $K$ ), and the small sample size-corrected AIC values ( $AIC_c$ ) for each model. Model notation includes the additive effects of S = section (above, within, or below the control or removal reaches), TL = length, W = weight, ST = state, CMS = discharge, and FTW = first 2 weeks.

Model	$\log(L)$	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
<b>GR <math>\times</math> CRR</b>					
$\varphi(S, TL) \psi(ST, CMS, TL, FTW)$	-5,510.79	30	11,082.54	0.00	0.27
$\varphi(S) \psi(ST, CMS, FTW)$	-5,512.85	28	11,082.55	0.01	0.27
$\varphi(S, W) \psi(ST, CMS, TL, FTW)$	-5,511.44	30	11,083.84	1.30	0.14
$\varphi(S, TL) \psi(ST, CMS, FTW)$	-5,512.83	29	11,084.56	2.02	0.10
$\varphi(S, W) \psi(ST, CMS, FTW)$	-5,512.84	29	11,084.59	2.05	0.10
$\varphi(S) \psi(ST, CMS, TL, FTW)$	-5,512.85	29	11,084.60	2.06	0.10
$\varphi(S, TL) \psi(ST, CMS, TL)$	-5,514.49	29	11,087.89	5.36	0.02
$\varphi(S, TL) \psi(ST, CMS)$	-5,516.54	28	11,089.93	7.39	0.01
$\varphi(S) \psi(ST, CMS, TL)$	-5,520.07	28	11,096.98	14.45	< 0.01
$\varphi(S) \psi(ST, CMS)$	-5,521.23	27	11,097.24	14.70	< 0.01
$\varphi(S, W) \psi(ST, CMS, TL)$	-5,519.64	29	11,098.18	15.64	< 0.01
$\varphi(S, W) \psi(ST, CMS)$	-5,521.22	28	11,099.28	16.74	< 0.01
<b>GR <math>\times</math> HL</b>					
$\varphi(S) \psi(ST, CMS, TL, FTW)$	-3,969.38	29	7,997.64	0.00	0.28
$\varphi(S, TL) \psi(ST, CMS, TL, FTW)$	-3,968.45	30	7,997.86	0.23	0.25
$\varphi(S, W) \psi(ST, CMS, TL, FTW)$	-3,968.53	30	7,998.02	0.38	0.23
$\varphi(S, TL) \psi(ST, CMS, FTW)$	-3,970.28	29	7,999.45	1.80	0.11
$\varphi(S, W) \psi(ST, CMS, FTW)$	-3,970.42	29	7,999.73	2.09	0.10
$\varphi(S) \psi(ST, CMS, FTW)$	-3,972.27	28	8,001.37	3.73	0.04
$\varphi(S) \psi(ST, CMS, TL)$	-3,981.30	28	8,019.43	21.79	< 0.01

downstream of the reaches. Survival probabilities within the reaches probably represent true survival probabilities because an individual could not permanently emigrate from the reach without being subject to detection. Conversely, apparent survival probabilities in the sections upstream and downstream of the reaches probably reflect permanent emigration, which could not be differentiated from true survival in our study. Apparent survival did not differ in the sections upstream or downstream of the reaches for either cross (Figure 4). Although fish length and weight appeared to have an effect on apparent survival, the relationship was weak, and the associated 95% CIs overlapped zero (GR  $\times$  CRR:  $\hat{\beta}_{TL} = 0.003$  [-0.0009, 0.007] and  $\hat{\beta}_{weight} = 0.001$  [-0.002, 0.004]; GR  $\times$  HL:  $\hat{\beta}_{TL} = 0.004$  [-0.002, 0.011] and  $\hat{\beta}_{weight} = 0.005$  [-0.003, 0.013]).

### Rainbow Trout Movement

Movement probabilities for both the GR  $\times$  CRR and GR  $\times$  HL were most affected by state and discharge, both of which appeared in the top models for both crosses (Table 3). Model selection results also suggested that movement probabilities were lower in the first 2 weeks of the study period than in

subsequent weeks (GR  $\times$  CRR:  $\hat{\beta}_{FTW} = -0.40$  [-0.46, -0.35] and GR  $\times$  HL:  $\hat{\beta}_{FTW} = -0.54$  [-0.76, -0.33]). Fish length exhibited a weak relationship with movement in both the GR  $\times$  HLs ( $\hat{\beta}_{TL} = 0.009$  [0.001, 0.016]) and GR  $\times$  CRRs ( $\hat{\beta}_{TL} = -0.007$  [-0.008, -0.007]).

Model-averaged initial movement probabilities out of the reaches was similar for the GR  $\times$  CRR, whereas movement out of the control reach was higher than out of the removal reach for the GR  $\times$  HL (Figure 5). For both crosses, movement was lower for the weeks in which discharge was high (>1.98 m<sup>3</sup>/s; August 19 to September 23). Patterns of secondary movement suggest that both crosses were more likely to return to the removal reach than the control reach for both GR  $\times$  CRRs (control = 0.67 [SE, 0.09], removal = 0.92 [SE, 0.02]) and GR  $\times$  HLs (control = 0.51 [SE, 0.30], removal = 0.95 [SE, 0.01]).

### Rainbow Trout Abundance

The Rainbow Trout population in both reaches decreased between August and October 2010. Decreases in abundance were larger for both crosses in the control reach than in the removal reach, supporting the movement data suggesting that

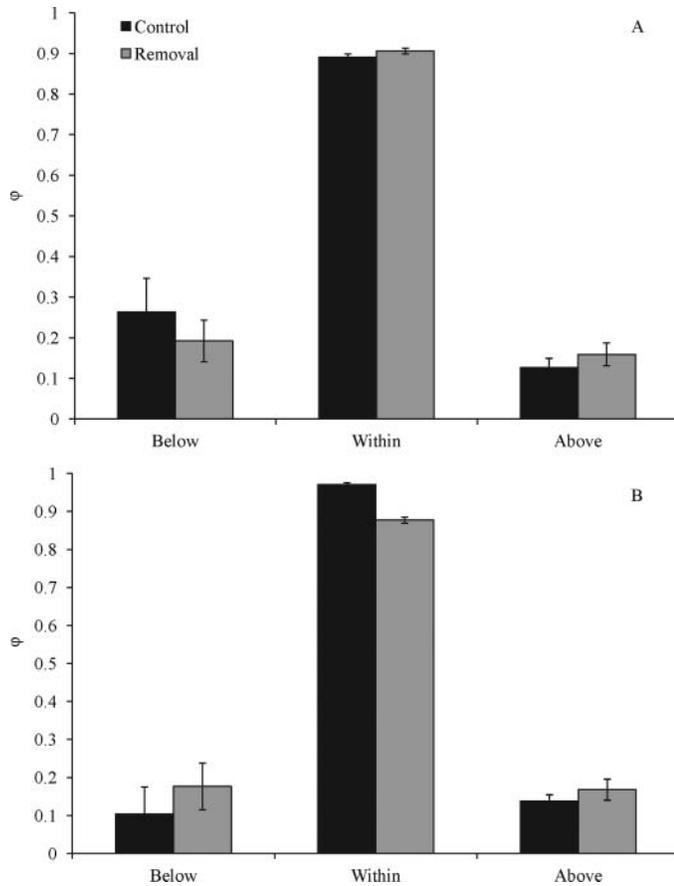


FIGURE 4. Model-averaged (bars = SEs) weekly apparent survival probabilities ( $\phi$ ) for two Rainbow Trout crosses—(A) GR  $\times$  CRR, and (B) GR  $\times$  HL (see Figure 1)—below, within, and above the control and Brown Trout removal reaches in the Cache la Poudre River, Colorado.

Rainbow Trout were more likely to return to the removal reach following initial movements out of the reaches. An estimated 509 (SE = 35) Rainbow Trout (26% of those stocked in August) remained in the control reach in October, with approximately 32% of the GR  $\times$  CRRs ( $\hat{N} = 312$  [SE = 17]) and 20% of the GR  $\times$  HLs ( $\hat{N} = 196$  [SE = 27]) remaining. Conversely, an estimated 1,428 (SE = 63) Rainbow Trout (72% of those stocked in August) remained in the removal reach in October, with approximately 93% of the GR  $\times$  CRRs

( $\hat{N} = 914$  [SE = 32]) and 52% of the GR  $\times$  HLs ( $\hat{N} = 513$  [SE = 14]) remaining. These results also support the movement data suggesting that the GR  $\times$  HLs had a higher probability of movement out of the control than the removal reach.

### Brown Trout Apparent Survival

Apparent survival probabilities of Brown Trout were affected by section, fish length, and fish weight (Table 4). Survival was most affected by section, appearing in all supported models within the set. Brown Trout survival was lower for fish within the removal reach than fish within the control reach (Figure 6). Apparent survival probabilities for Brown Trout in the sections above the reaches were lower than those in the sections below the reaches. Comparing longitudinally in the removal reach, survival of fish within the reach did not differ from that of fish upstream. However, survival of fish downstream was higher than for those fish either within or upstream of the reach. Comparing longitudinally in the control reach, survival of fish within the reach did not differ from that of fish downstream, although survival of fish upstream was lower than that of fish within or downstream of the reach (Figure 6). Fish length and weight also had some influence on apparent survival probabilities. Estimates of the effect size and associated 95% CIs from the top models including length or weight suggested a positive, but small relationship with both length ( $\hat{\beta}_{TL} = 0.002$  [0.0004, 0.005]) and weight ( $\hat{\beta}_{weight} = 0.001$  [0.0003, 0.002]).

### Brown Trout Movement

Movement probabilities for Brown Trout during the primary study period were most affected by discharge, differences in the first 2 weeks, and the interaction between state and spawn, all of which appeared in the top models of the set (Table 4). Brown Trout moved into both reaches. Movement into the removal reach was higher than into the control reach, especially during the first and third weeks of the study. Discharge negatively affected movement ( $\hat{\beta}_{CFS} = 0.0278$  [95% CI, 0.0276, 0.0279]), more movement occurring during low rather than high discharge periods. Movement probabilities for all movement states were also higher during the Brown Trout

TABLE 4. Model selection results for multistate models fit to wild PIT-tagged Brown Trout data from the Cache la Poudre River, Colorado. The candidate model set included over 300 models with various structures for apparent survival ( $\phi$ ) and movement ( $\psi$ ). Further details are provided in Table 3.

Model	$\log(L)$	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
$\phi(S, W) \psi(ST \times SP, CMS, FTW)$	-3,056.20	61	6,241.89	0.00	0.52
$\phi(S, W) \psi(ST \times SP, CMS, TL, FTW)$	-3,056.03	62	6,243.80	1.90	0.20
$\phi(S, L) \psi(ST \times SP, CMS, FTW)$	-3,057.32	61	6,244.14	2.25	0.17
$\phi(S, L) \psi(ST \times SP, CMS, TL, FTW)$	-3,057.22	62	6,246.18	4.29	0.06
$\phi(S) \psi(ST \times SP, CMS, FTW)$	-3,060.19	60	6,247.62	5.72	0.03
$\phi(S) \psi(ST \times SP, CMS, TL, FTW)$	-3,059.57	61	6,248.64	6.75	0.02

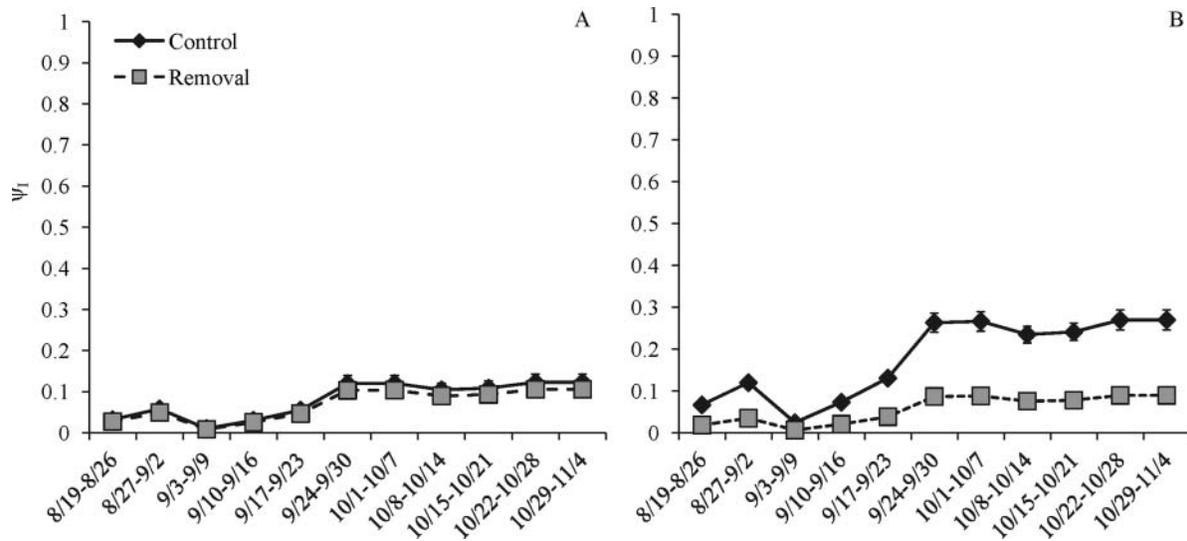


FIGURE 5. Initial movement probabilities ( $\psi_i$ ; bars = SEs) for two Rainbow Trout crosses—(A) GR  $\times$  CRR, and (B) GR  $\times$  HL (see Figure 1)—calculated as the sum of movements out of control reach downstream (C  $\rightarrow$  A) and upstream (C  $\rightarrow$  D) and out of the removal reach downstream (R  $\rightarrow$  F) and upstream (R  $\rightarrow$  H) in the Cache la Poudre River, Colorado.

spawning period than the prespawning period (Figure 7). Secondary movement into or out of the control or removal reaches was similar, suggesting that Brown Trout were in a state of equilibrium in both reaches following initial movement past the antenna stations.

### Brown Trout Abundance

Brown trout abundance changed in both reaches between August and October 2010. In the removal reach, as the movement data suggested, the Brown Trout population increased from the estimated 90 (SE = 49) remaining in the section following the removal to 782 (SE = 38) Brown Trout in October. In the control reach, the Brown Trout population experienced

a 53% decline in abundance between August and October, dropping from 1,679 (SE = 451) in August to 770 (SE = 41) Brown Trout in October, suggesting that the addition of Rainbow Trout to this reach induced a negative change in Brown Trout abundance.

### DISCUSSION

Recovery of wild Rainbow Trout populations in Colorado is dependent on development of Rainbow Trout that are resistant to *Myxobolus cerebralis* and the ability of these fish to survive and reproduce in the presence of abundant Brown Trout populations. While existing Rainbow Trout crosses exhibit resistance to *M. cerebralis* (Schisler et al. 2006; Fetherman et al. 2012), our results suggest the Brown Trout removal did not positively influence apparent survival of these crosses. Instead our results suggest that short-term apparent survival of Rainbow Trout and Brown Trout was affected by size-specific effects of competition, which for both the Brown Trout and GR  $\times$  HLs resulted in lower survival in the removal section. Movements of Brown Trout and Rainbow Trout were related to discharge, lower movement probabilities occurring during periods of high discharge. Handling and tagging also influenced movement, which was lower during the first 2 weeks than in subsequent weeks. In addition, spawning increased movement probabilities for Brown Trout. As expected, brown trout abundances increased in the removal section as fish recolonized the reach. However, in the control section, the introduction of rainbow trout had a negative effect on the Brown Trout population. Initial movement data showed that fewer GR  $\times$  HLs moved out of the removal reach than control reach, but this was not the case for the GR  $\times$  CRRs.

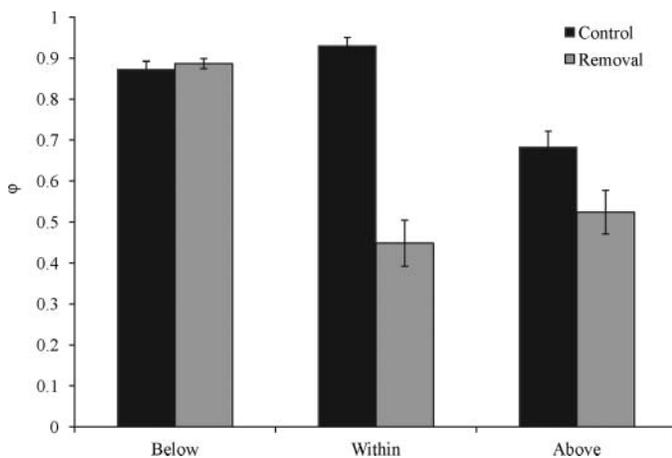


FIGURE 6. Model-averaged weekly apparent survival probabilities ( $\phi$ ; bars = SEs) for Brown Trout below, within, and above the control and removal reaches in the Cache la Poudre River, Colorado.

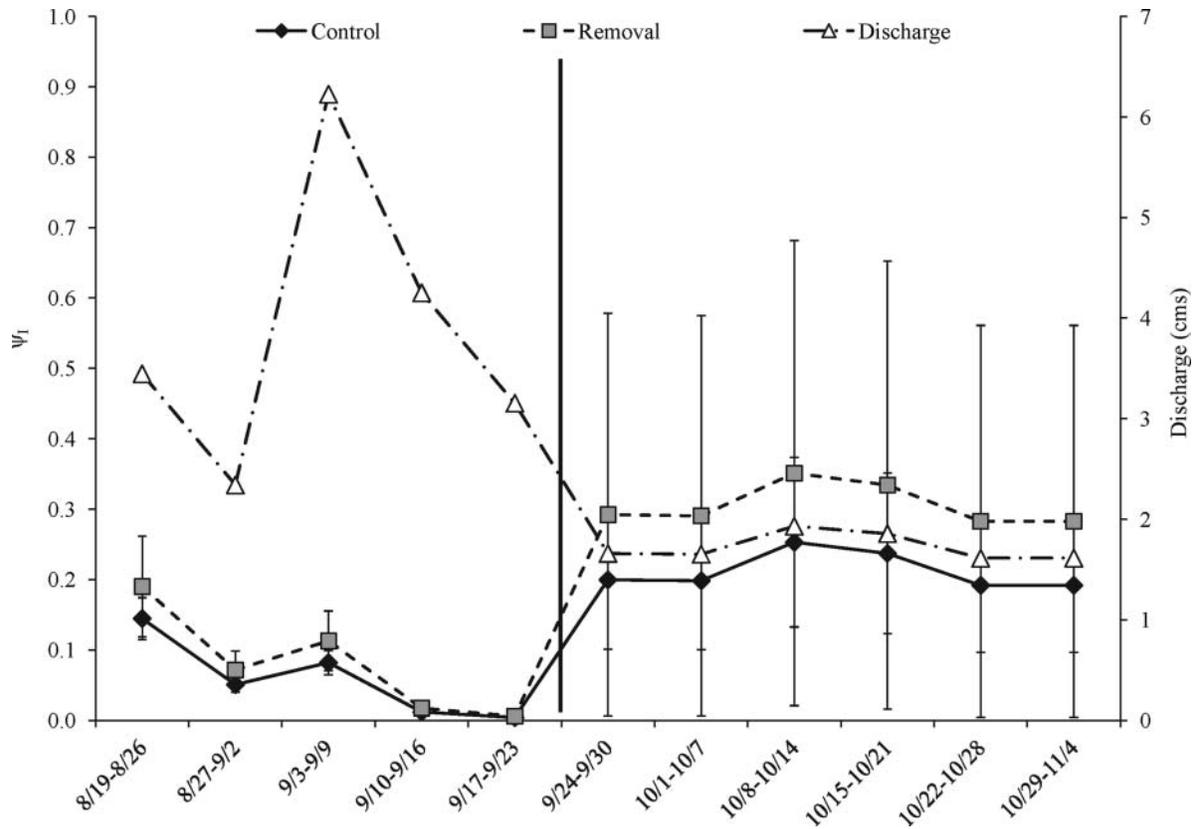


FIGURE 7. Brown Trout net initial movement probabilities ( $\psi_i$ ; bars = SEs) into the control and removal reaches in the Cache la Poudre River, Colorado. Discharge and spawn had a large effect on Brown Trout movement probabilities, as evident by the solid black vertical line on September 24, which denotes the transition from prespawn to spawning period.

However, abundance and secondary movement estimates suggested that Rainbow Trout were more likely to return to the removal reach after initial movements out of the reaches, suggesting that Brown Trout removal may have positively influenced short-term retention of Rainbow Trout.

Analogous to the establishment of an invasive species, reintroduced Rainbow Trout are subject to the three basic phases of the invasion process: arrival or introduction, establishment, and integration (Vermeij 1996). Introduction in this case was facilitated by stocking Rainbow Trout into locations from which they had been eliminated by whirling disease, and introduction success was partially dependent upon the inherent characteristics of the Rainbow Trout (Townsend 1996). For example, the GR  $\times$  CRR cross was developed using the Colorado River Rainbow Trout strain, a wild strain that had been widely stocked in Colorado and composed many of the naturally reproducing wild Rainbow Trout fisheries prior to the establishment of *M. cerebralis* (Walker and Nehring 1995). The relatively high survival probabilities of the GR  $\times$  CRR within both the control and removal reaches, and the relatively low initial movement out of the reaches, is consistent with historical observations regarding the wild parental CRR background of the GR  $\times$  CRR. Historical ratios of Rainbow Trout to Brown Trout in the Cache la Poudre River (60:40; Klein

1963) suggest that the CRR strain was able to survive and reproduce in the wild despite the presence of Brown Trout. Overall, Brown Trout removal did not appear to influence short-term survival or movement of GR  $\times$  CRRs, suggesting that, like the parental CRR strain, the GR  $\times$  CRR was well suited for river reintroductions.

The GR  $\times$  HLs showed a greater preference than the GR  $\times$  CRRs for areas in which Brown Trout had been removed. Initial movements out of the control reach were higher than from the removal reach. In addition, secondary movement back into the removal reach was higher than into the control reach, and GR  $\times$  HL abundance was higher in the removal reach in October, suggesting that the GR  $\times$  HL were more likely to return to and be retained in the reach where Brown Trout abundance was lower. Taken together, these results suggest that Brown Trout removal had a positive effect on the GR  $\times$  HL populations, which have exhibited low apparent survivals in other river reintroductions in Colorado. The results suggest that this is to be expected unless predator removal occurs. Because the GR  $\times$  HLs exhibit lower mortality and myxospore development following exposure to *M. cerebralis* than do other Rainbow Trout strains (Fetherman and Schisler 2012; Wagner et al. 2012), and the parental Harrison Lake strain is a well-established lake fish (Wagner et al. 2006), GR  $\times$  HLs

would probably be better utilized in lake rather than river reintroductions in Colorado and elsewhere.

Successful introduction and establishment of a species is also dependent upon the characteristics of the receiving community (Townsend 1996). Newly arriving or introduced species may experience ecological resistance (Elton 1958), consisting of three interacting elements: environmental, biotic, and demographic resistance (Moyle and Light 1996; Vermeij 1996). Reduction of biotic resistance through Brown Trout removal was the primary focus of our study. The increase in Brown Trout densities following the introduction of *M. cerebralis* (Baldwin et al. 1998; Nehring and Thompson 2001) suggests that Brown Trout may have expanded to fill the biological niche vacated by the Rainbow Trout (Baldwin et al. 1998). The introduction of Rainbow Trout to rivers in which these populations are established could result in changes in the frequency of competitive interactions, levels of food availability, or a functional response to predators; it could also influence the growth and survival of wild fish (Einum and Fleming 2001). The addition of large numbers of fish in limited habitat also inevitably affects population density (Einum and Fleming 2001), as well as any density-dependent characteristics of the environment or the fish themselves (Elliott 1989). This effect could account for the lower survival rates of Brown Trout returning to the removal reach, where competitive interactions probably changed due to Rainbow Trout establishment in the absence of Brown Trout.

Competitive interactions in the control reach probably favored the better established Brown Trout population. Rainbow trout exhibit niche shifts away from preferred Brown Trout habitat when the two species occur in sympatry, and as a result, Rainbow Trout are forced into areas with deficiencies such as higher water velocities, greater distance from cover, or lower food availability (Gatz et al. 1987). As such, we expected that Rainbow Trout would have difficulty competing with the expanded Brown Trout populations in the control reach, and this competition is one likely explanation for the higher movement rates observed in the control reach for GR  $\times$  HLs. However, Brown Trout in the control reach were not immune to the effects of the increase in overall fish abundance due to Rainbow Trout introduction because October abundance estimates showed that the addition of Rainbow Trout to the control reach also appeared to cause a reduction in Brown Trout abundance.

The timing of the removal and the behavior of the Brown Trout population itself may have also increased the biotic resistance of the system to Rainbow Trout establishment and explain the Brown Trout abundance changes observed in the control reach. Brown Trout typically occupy the same core area and exhibit little movement, except during the spawning season (Solomon and Templeton 1976; Burrell et al. 2000), during which time they exhibit increased activity and extensive movements associated with spawning (Burrell et al. 2000; Bettinger and Bettoli 2004; James et al. 2007). We observed an increase in movement in both reaches during periods of low discharge and during the Brown Trout spawning

period, which was associated with higher rates of movement out of the sections by both crosses of Rainbow Trout. In addition, Brown Trout have been shown to return to their home ranges following artificial displacement (Halvorsen and Stabell 1990). As a result, the Brown Trout removal did not appear to change short-term Rainbow Trout survival or movement rates to the extent we expected. However, it is important to note that we had only one control reach and one removal reach, so effects of the removal may have been more apparent if replication of the reaches had been possible.

Mechanical removals of piscivorous fish species have been used to promote the survival of target species in other systems across the USA with varying degrees of success. In West Long Lake, Nebraska, a 3-year removal of Northern Pike *Esox lucius* was successful in altering the size structure of the Yellow Perch *Perca flavescens* and increasing the relative abundance and size structure of the Bluegill *Lepomis macrochirus* (Jolley et al. 2008). The relative abundance of six native littoral species increased within 2 years as a result of a 6-year removal of Smallmouth Bass *Micropterus dolomieu* from Little Moose Lake in the Adirondacks (Weidel et al. 2007). Additionally, repeated yearly removals in the Colorado River have resulted in declines in large nonnative predators (McAda 1997; Brooks et al. 2000; Modde and Fuller 2002). These studies suggest that mechanical removal can be utilized to obtain desired changes in predator and prey dynamics in established wild systems.

Several factors must be considered when determining whether mechanical removal is necessary and has the potential to be successful. The first consideration is whether the removal is necessary for the reintroduction and establishment of the target species. In our case, the data suggest that Brown Trout removal did not dramatically effect apparent survival or emigration from the study site. The long-term goal of the resistant Rainbow Trout reintroduction program is to produce and maintain self-sustaining whirling disease resistant Rainbow Trout populations in Colorado waters in which there is a high prevalence of *M. cerebralis* infection (Schisler et al. 2006; Fetherman et al. 2011; Fetherman et al. 2012). Models examining the interactions between Rainbow Trout introduction size (propagule pressure [Townsend 1996]) and demographic resistance [Moyle and Light 1996], environmentally stochastic *M. cerebralis* exposure rates, and Brown Trout population size (biotic resistance; Moyle and Light 1996) suggest that a single introduction of Rainbow Trout will not result in a self-sustaining Rainbow Trout population in rivers like the Cache la Poudre River (Fetherman 2013). Therefore, multiple reintroductions, with or without Brown Trout removal, will probably be needed to overcome ecological resistance factors and to realize long-term positive effects of Brown Trout removal in Colorado's rivers.

The second consideration is whether the removal will be successful after one removal effort, or if multiple removal efforts are needed to overcome biotic resistance. For example,

a single removal of 66% of the Brown Trout population in the Au Sable River in Michigan did not result in population or size at age increases in the sympatric Brook Trout population (Shetter and Alexander 1970). Movement probabilities of Brown Trout in the removal reach in our study suggest that Brown Trout returned to the reach fairly quickly. Therefore, the observed short-term benefits of the one-time removal may not necessarily translate to a continued positive response in reintroduced Rainbow Trout populations over the long term.

Exposure to *M. cerebralis* also contributes to biotic resistance (Moyle and Light 1996) and could result in low survival in reintroduced Rainbow Trout populations because disease can interact with predation to have an even larger effect on survival. Exposure to disease has been shown to increase susceptibility to predation (Seppälä et al. 2004), and diseased prey are often eaten in higher than expected proportions due to increased prey vulnerability or active predator selection (Mesa and Warren 1997). Parasites also lower the energy reserves of their host (Poulin 1993), and parasitized fish often take more risks to feed in the presence of a predator than do unparasitized fish (Milinski 1985; Godin and Sproul 1988). Therefore, compounding effects of disease exposure and increased susceptibility to predation may lead to lower survival in locations where *M. cerebralis* and predator abundance (aquatic or terrestrial) is high.

A third consideration is whether environmental resistance factors (temperature, flow, abiotic resources; Moyle and Light 1996) may prevent the removal from being a success. Reintroductions in Colorado occur in rivers that have large annual fluctuations in water flow and temperature. Rivers like the Colorado and Cache la Poudre rivers can experience extensive low-flow periods during the summer months (USGS 2009), and minimum discharge has been shown to have a large effect on the survival of reintroduced Rainbow Trout (Fetherman et al. 2014). Lower flows result in higher summer water temperatures and lower dissolved oxygen levels (Williams et al. 2009), both of which can directly affect salmonid survival (Hicks et al. 1991). Biotic resistance may also be increased as a result of low flows and high temperatures. Increased stress due to low flow may intensify the effects of *M. cerebralis* infection, and ectoparasite infestation has been shown to peak during periods of low flow and high mean water temperature, potentially significantly increasing mortality in these rivers (Schisler et al. 1999). Low flows also reduce suitable habitat and can lead to high densities and overcrowding, increased predation, and increased competition (Arisemendi et al. 2012).

Finally, managers must weigh the cost of the removal against the benefits of the action. For example, nearly \$4.4 million has been spent to mechanically remove >1.5 million nonnative predatory fish from the Colorado River; however, 86% of published reports (as of 2005) suggested that native species did not benefit from the removal efforts (Mueller 2005). Additionally, the logistic constraints associated with large removal efforts may be limiting. In our study, over 100 volunteers helped to remove 89% of the Brown Trout population from a 1.0-km

reach of the Cache la Poudre River. Assembling and maintaining this large of a volunteer base for removals of the same size in multiple locations, or a removal effort over longer distances, presents enormous logistical challenges.

Although our results suggest that Brown Trout removal did have a positive effect on the short-term retention of the GR × HLs, the overall benefit of the removal is equivocal. Due to the logistical constraints of conducting removals in other large river systems in Colorado, the return of Brown Trout to the removal reach, and the fact that removal did not appear to have an effect on the survival of either cross or the movement of the GR × CRRs, we conclude that adult Brown Trout removal is not a viable management option to pursue in future *M. cerebralis*-resistant Rainbow Trout introductions in Colorado. The stocked Rainbow Trout seem to be capable of overcoming many of the ecological resistance factors encountered, potentially becoming established in both reaches of the Cache la Poudre River. Further study is needed to determine if Rainbow Trout have become established, exhibit long-term persistence, and are integrated into the Cache la Poudre River ecosystem, and this research is ongoing. Additional research should also focus on Rainbow Trout reintroduction strategies, with regard to fish size, reintroduction density, and the number of reintroductions needed to produce a self-sustaining rainbow trout population in Colorado.

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