THESIS

SURVIVAL OF RAINBOW TROUT FRY IN THE WILD: A COMPARISON OF TWO WHIRLING DISEASE RESISTANT STRAINS

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ABSTRACT

SURVIVAL OF RAINBOW TROUT FRY IN THE WILD: A COMPARISON OF TWO WHIRLING DISEASE RESISTANT STRAINS

Many animal populations have experienced population declines due to a broad range of factors such as habitat loss and degradation, invasive species, disease, and climate change. Introduced pathogens are known to have dramatic effects on populations. Following the establishment of the parasite that causes whirling disease (*Myxobolus cerebralis*) in Colorado, Colorado Parks and Wildlife (CPW) developed a whirling disease resistant Rainbow Trout (*Oncorhynchus mykiss*) for stocking known as the GRxCRR. The GRxCRR is a cross between the wild, susceptible Colorado River Rainbow (CRR) and the domesticated, resistant German Rainbow (GR) trout strains. It was thought that the GRxCRR would exhibit survival and reproduction similar to that of the CRR, overcome potential disadvantages associated with the history of domestication of the GR, and maintain the genetic resistance to whirling disease of the GR. One disadvantage to stocking GRxCRR is the potential for outcrossing and backcrossing that could decrease resistance to whirling disease. Stocking pure GR was not considered a viable option because it was thought that they would not survive well in a natural environment. However, in a laboratory study the GR and GRxCRR strains showed few physiological differences, indicating that the GR may be a candidate for stocking in whirling disease positive streams. I undertook a laboratory and field experiment to compare fry survival between the two strains. The field experiment was conducted in three drainages (Cache la Poudre River, Middle Fork of the South Platte River, and Colorado River), and three streams were selected in each drainage. One-mile reaches of each stream were stocked in August 2014 with 5,000 GRxCRR, identified with coded wire tags, and 5,000 untagged GR. In October 2014, April 2015 and August 2015, population estimates were conducted, providing an estimate of apparent survival for each strain. Two laboratory experiments were also conducted. In the first experiment, a 50:50 mix of GRxCRR and GR were stocked into large open mesocosms with one wild Brown Trout (*Salmo trutta*) predator. Survival was estimated over a 24-hour time period. The second experiment was similar, but I added treatments with or without cover. The field experiment revealed that apparent survival and growth rate was influenced by strain, stream, and primarily average temperature within the first year after stocking. After two months in the wild, the GRxCRR exhibited a higher growth rate than the GR, opposite of what is seen in the hatchery. However, after 12 months there was no significant difference in apparent survival or growth rate between the GR and GRxCRR. Laboratory experiments revealed that there were no differences in survival between the strains when confronted with Brown Trout predation. My results indicate that the GR may be a viable alternative for stocking in streams that contain *M. cerebralis*.

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INTRODUCTION

Many animal populations have experienced population declines due to a broad range of factors such as habitat loss and degradation, invasive species, disease, and climate change (Gibbons et al. 2000; Edwards and Richardson 2004; Both et al. 2006; Carpenter et al. 2008). Introduced pathogens are known to have dramatic effects on populations. For instance, the introduction of the malarial parasite *Plasmodium relictum capistranoae* resulted in extinctions of many native Hawaiian avifauna (van Riper et al. 1986), chytridiomycosis has resulted in amphibian population declines (Berger et al. 1998; Weldon et al. 2004; Skerratt et al. 2007), and rabbit haemorrhagic disease significantly reduced wild rabbit populations in Spain (Villafuerte et al. 1995). In fish populations, introduction of diseases and parasites has also led to mortality and declines in wild populations. Viral hemorrhagic septicemia (VHS) has been associated with large mortality events of freshwater Drum (*Aplodinotus grunniens*) and other fish species in the Great Lakes (Lumsden et al. 2007; Bowser 2009). Salmon lice (*Lepeophtheirus salmonis*) infection in wild Pink Salmon (*Oncorhynchus gorbuscha*) caused population declines and could potentially lead to future local extinction (Krkosek et al. 2007).

The almost total loss of wild Rainbow Trout (*Oncorhynchus mykiss*) from several intermountain-west states has been linked to the introduction of *Myxobolus cerebralis*, the myxozoan parasite responsible for salmonid whirling disease. Significant loss of Rainbow Trout fry populations in Colorado and Montana was documented following the establishment of *M. cerebralis* in the Gunnison River, Colorado (Nehring and Walker 1996) and Madison River, Montana (Vincent 1996). In Colorado, the parasite has become established in most coldwater systems with similar negative effects on Rainbow Trout as seen in the Gunnison River (Nehring and Walker 1996; Nehring and Thompson 2001). Age-0 salmonids, in which skeletal ossification has not occurred, are particularly susceptible to infection and mortality (Halliday 1973; Markiw and Wolf 1983; Wolf et al. 1986; Markiw 1989; El-Matbouli et al. 1992; El-Matbouli et al. 1995) and age-0 recruitment failure is largely responsible for the overall population collapse of wild Rainbow Trout fisheries throughout Colorado (Nehring and Thompson 2001).

Before the introduction and establishment of *M. cerebralis*, most coldwater fisheries in Colorado were dominated by Rainbow Trout (a 60:40 ratio of Rainbow Trout to Brown Trout [*Salmo trutta*]) but are now predominantly Brown Trout (Klein 1963). Brown Trout are less susceptible to the parasite probably due to their evolutionary history with the parasite in their native European range (Granath et al. 2007).

The complex multistage life cycle of the parasite requires two hosts, a salmonid and the oligochaete *Tubifex tubifex*, making it very difficult to eradicate *M. cerebralis* once it has become established. Snieszko (1974) describes three main factors that affect disease transmission and, ultimately control options: the environment, the host(s), and the pathogen. Manipulating one or more of the three factors is necessary to control or eradicate any pathogen responsible for causing disease. Initially, whirling disease was considered a hatchery disease and it was possible to manipulate all three factors in this controlled environment. Environmental manipulations included dewatering hatcheries to eradicate the free-living forms of the parasite (Wagner et al. 2002), ceasing the use of earthen ponds that provided habitat for *T. tubifex*, and switching production to concrete-lined raceways. Infected fish hosts were removed from hatcheries to control the pathogen (*M. cerebralis*) and disinfectants such as calcium cyanamide, lime or chlorine were used to eradicate the free-living forms of the parasite (Hoffman and Putz 1969; Hoffman and Hoffman 1972; Schaperclaus 1986). Once facilities were disinfected, water sources were switched from surface water to well water to avoid re-infection (Hedrick et al. 1998).

Clearly, manipulations used in hatcheries are not realistic in most wild settings and other options to reduce parasite transmission and survival, such as vaccination or other contraceptive means, are also not viable in the wild or do not exist for *M. cerebralis*. Therefore, manipulating or using existing host resistance was thought to be the most realistic option to disrupt the parasite life cycle in wild populations (El-Matbouli et al. 1999; Kerans et al. 1999; Beauchamp et al. 2002; Schisler 2006; Wagner et al. 2006; Fetherman et al. 2011, 2012; Nehring et al. 2013, 2016). Resistant *T. tubifex* lineages have been identified and were associated with reductions in parasite production (Beauchamp et al. 2005; Nehring et al. 2013). For instance, the number of triactinomyxons (TAMS), the waterborne, free-living infective stage of the parasite, declined dramatically below Windy Gap Reservoir after the *T. tubifex* community structure naturally changed from susceptible linages to more disease-resistant lineages (Nehring et al. 2013). Two attempts were made to intentionally manipulate *T. tubifex* community composition by introducing whirling disease resistant *T. tubifex* lineages but those efforts did not dramatically reduce parasite prevalence (Clapp 2009; Winkelman and Gigliotti 2014). Due to the limited success with using resistant *T. tubifex*, additional management and research efforts focused on the potential stocking of Rainbow Trout genetically resistant to the parasite (Fetherman et al. 2014).

The Colorado River Rainbow Trout strain (CRR) was historically used to stock and establish Rainbow Trout populations in Colorado and the self-sustaining population in the Upper Colorado River (Middle Park, Colorado) was used as a brood stock for Colorado's stocking program (Thompson et. al. 2002). However, the CRR was highly susceptible to *M. cerebralis* and continued stocking of this strain following the establishment of the parasite was unsuccessful in reestablishing wild Rainbow Trout fisheries. The need for a new management option led Colorado Parks and Wildlife (CPW) to research the efficacy of using whirling disease resistant Rainbow Trout (Schisler et al. 2006). A whirling disease resistant Rainbow Trout was discovered in a Bavarian hatchery in Germany that presumably developed resistance to whirling disease by being continuously exposed to *M. cerebralis* for over a century (El-Matbouli et al. 2002). The German Rainbow strain (referred to hereafter as GR) is more resistant to whirling disease than many other Rainbow Trout strains found in North America (Hedrick et al. 2003).

Due to the high degree of domestication of the GR, over a hundred years in a hatchery setting (El-Matbouli et al. 2002; Hedrick et al. 2003), it was thought that their survival in the wild might be lower than that of other Rainbow Trout strains that had been historically stocked in Colorado (Schisler et al. 2006). One specific concern was that hatchery-reared GR would be predator naïve and particularly susceptible to predation, resulting in lower survival in the wild (Suboski and Templeton 1989; Brown and Laland 2001; Brown et al. 2003). As a strategy to potentially increase survival of stocked Rainbow Trout, CPW started a breeding program using the resistant GR and the susceptible Colorado River Rainbow (CRR). CPW's goal was to produce a Rainbow Trout cross that retained the whirling disease resistance of the GR while gaining the survival and reproduction of the CRR (Schisler et al. 2006). The cross was referred to as the GRxCRR.

Since 2008, the GRxCRR has been stocked in all major Colorado coldwater drainages to reestablish Rainbow Trout populations. Larger (≥ 150 mm total length [TL]) GRxCRRs were initially stocked into Colorado rivers for two reasons: 1) they are less susceptible to *M. cerebralis* because their skeleton is largely ossified at this size (Ryce et al. 2005) and 2) they are less susceptible to predation because they exceed the gape limit of most natural aquatic predators (Fetherman et al. 2014). However, survival of larger GRxCRR was low and there was little evidence of recruitment (Fetherman et al. 2014). More recently, GRxCRR fry (< 100 mm TL) have been stocked into river systems. The strategy of stocking fry attempts to increase survival by reducing hatchery related behavioral conditioning (Olla et al. 1998; Jackson and Brown 2011). Stocked fry have started to recruit to older age classes in, the Colorado and Gunnison Rivers, the two river systems where the majority of the whirling disease research has occurred in Colorado (Fetherman and Schisler 2016).

Observed survival of stocked GRxCRR fry is promising; however, it is known that outcrossing and backcrossing of GRxCRR can produce lower resistance and increased variability in resistance (Fetherman et al. 2011; Fetherman et al. 2012). If wild reproduction occurs, the potential for reduced resistance could slow recovery efforts. Outcrosses and backcrosses are still more resistant than pure CRR (Fetherman et al. 2011), but their resistance is more variable, resulting in higher average myxospore counts per fish, which could reduce survival (Fetherman et al. 2012). Additionally, increased myxospore production has the potential to increase infection prevalence and severity throughout the population, further suppressing survival and recruitment, and potentially hampering efforts to create self-sustaining populations. One option to overcome the loss of resistance associated with GRxCRR reproduction is to stock pure GR. However, as mentioned above, there was uncertainty about the survival of the GR strain in the wild due to its domestic history. Despite those concerns, laboratory comparisons showed that exposure to *M. cerebralis* did not produce differences in growth or swimming ability between the GR and

GRxCRR (Fetherman et al. 2011), indicating that stocking pure GR could be an option for establishing whirling disease resistant Rainbow Trout that would retain resistance over generations.

The goal of my research was to determine if there were differences in survival between the GR and GRxCRR Rainbow Trout strains. To achieve this goal, I designed two experiments. The first experiment was a field study that evaluated potential differences in apparent survival between the GR and the GRxCRR when stocked into lotic systems. The second experiment was a laboratory study that evaluated potential differences in predation susceptibility between the GR and GRxCRR.

METHODS

Field Experiment

Stream survival evaluations were conducted in 1.6 kilometer (km) reaches of nine streams in Colorado between July 2014 and August 2015. The nine streams consisted of three streams in three separate drainages: 1) Lone Pine Creek, the North Fork of the Cache la Poudre River (N.F. Poudre), and Sheep Creek in the Cache la Poudre River drainage, 2) Spielberg Creek, Rock Creek, and Willow Creek in the Colorado River drainage, and 3) Jefferson Creek, Michigan Creek, and Tarryall Creek in the Middle Fork of the South Platte River drainage. Due to restricted stream access by the landowner the reach in Jefferson Creek was 0.7 km. All streams were coldwater systems with two or more fish species present and an average yearly temperature between 4.7 and 8 degrees Celsius. Streams ranged from 1,789 meters to 2,892 meters (m) in elevation and flowed through public and private land. Average stream width was between 3 and 8.8 m.

Streams were selected based on accessibility for stocking, and fish community structure. I assessed fish community structure before stocking and chose reaches that were dominated by Brown Trout. Brook Trout (*Salvelinus fontinalis*) were also present and large enough to be potential predators in several streams. When choosing streams, I made a visual qualitative assessment of habitat and selected streams of similar size and with similar physical characteristics. I did not make a quantitative assessment of stream habitat prior to Rainbow Trout stocking but did make detailed assessments of each stream as part of the study (see below).

Prior to the introduction of Rainbow Trout fry, two sampling sites (66 m, average length) were established in each stream reach, and fish population estimates were conducted in July 2014 utilizing three pass removal backpack electrofishing techniques (Temple and Pearsons 2007). I used these estimates to confirm that no Rainbow Trout were present prior to stocking, and to provide baseline data on initial fish assemblage composition, density, and biomass. In addition to Brown Trout and Brook Trout, other species that were commonly found included Longnose Sucker (*Catostomus catostomus*), White Sucker (*Catostomus commersonii*), Longnose Dace (*Rhinichthys cataractae*), Speckled Dace (*Rhinichthys osculus*) and Mottled Sculpin (*Cottus bairdii*). Less commonly encountered species were Johnny Darter (*Etheostoma nigrum*), Brook Stickleback (*Culaea inconstans*), Creek Chub (*Semotilus atromaculatus*) and Fathead Minnow (*Pimephales promelas*). The total biomass of fish species in each stream prior to stocking of Rainbow Trout ranged from 336 kilograms per hectare to 6,896 kilograms per hectare (Table 1).

Two strains of Rainbow Trout fry, GR and GRxCRR, were reared at the CPW Rifle Falls Fish Hatchery. To make field identification of each strain possible I marked the GRxCRR (n = 45,000) with coded wire tags (Northwest Marine Technology, Inc., Shaw Island, WA) and left the GR strain untagged. I decided not to tag the GR strain because I expected them exhibit lower survival in the wild due to their history of domestication and wanted to avoid further potential reduction in survival due to tagging. Coded wire tags were injected into the nose of anesthetized GRxCRR (tricaine methanosulfonate; MS-222) using two Mark IV automatic tag injectors (Northwest Marine Technology, Inc., Shaw Island, WA). Fish were then placed into a holding raceway to recover, and monitored for mortality for a 24-hour period following tagging during which time mortalities were removed, recorded, and replacement fish were tagged.

Based on the suggestions of CPW biologists who manage the streams in which these experiments were conducted, ten thousand Rainbow Trout fry, five thousand each of the GR and GRxCRR, were stocked into each of the streams between August 4 and 6, 2014. Fish were transported to each stream from the Rifle Falls Fish Hatchery in oxygenated fish transport trucks. Upon arrival, fish were placed in 19liter (L) buckets and acclimated to stream conditions by exchanging hatchery water with stream water. Once acclimated, fish were stocked by hand into the stream margins throughout the 1.6 km reach to attempt even distribution throughout available fry habitat.

I monitored post-stocking abundance of all fish species within my study streams at three time points: short-term (two months; August 2014 - October 2014), over-winter (six months; October 2014 – April 2015), and annual (twelve months; August 2014 – August 2015). I evaluated apparent survival, length, and growth rate of the GR and GRxCRR. I also estimated predator abundance, predator biomass, total biomass and competitor biomass. Population estimates were conducted at two sampling sites (66 m, average length) within the 1.6 km stocking reach in each of the study streams in October 2014 and August 2015. Due to hazardous access and unsafe sampling conditions, sampling occurred in only seven of the nine streams in April 2015. To assess apparent survival, I conducted population estimates using three pass removal backpack electrofishing techniques (Temple and Pearsons 2007). Removals were conducted using two to three Smith Root, Inc. LR-24 backpack electrofishing units depending on stream width. Electrofishing gear covered the wetted channel width, allowing for full coverage of all accessible trout habitat. Captured fish were kept in separate live-wells and sorted by pass until processing occurred. All Rainbow Trout captured were measured to the nearest millimeter (mm) and weighed to the nearest gram (g), and scanned for coded wire tags. I made the assumption that untagged Rainbow Trout were pure GR and tagged Rainbow Trout were GRxCRR. Although tag loss might bias my results, tag retention is generally above 90% when using coded wire tags (Ostergaard 1982; Elrod and Schneider 1986; Hale et al. 1998; Munro et al. 2003). At least 150 fish of every other species captured were measured to the nearest millimeter and weighed to the nearest gram. After 150 lengths and weights were recorded for a species, only lengths were recorded thereafter, and a length-weight regression was later used to assign weights. All fish were returned to the sampling site after processing.

Since quantitative assessment of stream habitat prior to Rainbow Trout stocking was not conducted, a suite of stream habitat characteristics were used to quantify potential differences among streams post stocking. Habitat measurements were taken after each sampling event in October 2014, April 2015, and August 2015. Starting at the bottom of each sampling site, width, depth, and flow measurements were taken at 0, 25, 50, 75 and 100% of the total sample site length. Depth and flow were measured perpendicular to the flow and at least ten depth and flow measurements were taken at equally spaced intervals. Depth was recorded to the nearest centimeter and flow (m/sec) was measured using a Marsh-McBirney Flo-mate 2000 flow meter at 60% of the depth. Elevation was measured using a Garmin Oregon 450 GPS unit and values were recorded at the bottom of each sampling site.

I also chose to measure temperature, pebble size, and entrenchment ratio because these metrics affect fish survival and growth (Pepin 1991; Selong et al. 2001; Suttle et al. 2004; Mazeika et al. 2006). Temperature was measured every 244 minutes using iButton® temperature loggers (Maxim Integrated, San Jose, CA) placed into or near each sampling site at the time of fry stocking. Loggers were housed in perforated half-inch PVC pipe and the PVC housing was attached with braided metal wire to rebar stakes that were embedded into the streambed. Measurements of entrenchment ratio and representative pebble counts were collected at every sampling station in August 2015. Entrenchment ratio (Figure 1)**,** was measured using a method adapted from Rosgen (1996) whereby bankfull stage and maximum depth at bankfull was determined, and the total width of the flood-prone area at two times the maximum depth, was measured for each sampling site. Resulting entrenchment ratio (E) was defined as:

$$E = \frac{W_F}{W_B}$$

where W_F is the width of the flood-prone area, and W_B is the width of the bankfull stage. A modified pebble count protocol was utilized by stratifying the length of the sampling station into 0, 25, 50, 75, and 100% transects of the sample site length. The width of twenty rocks were measured along the intermediate axis at evenly spaced intervals along each transect for a total of 100 rock width measurements taken over the entire sample section length (Wolman 1954). Pebble measurements were then placed into Wentworth size classes and converted into percentages to produce cumulative size distribution curves, resulting in the calculated percent smaller than size values (D_{15}, D_{35}, D_{50}, and D_{84}) for each sampling site.

Fish species abundance was estimated within each sampling site using the three pass removal estimates described by Seber and Whale (1970), and then extrapolated to average abundance within each 1.6 km reach. Apparent survival, the survival of individuals that were alive and remained within the study area, for the GR and GRxCRR was then calculated for the three different time periods: short-term

(August 2014 – October 2014), over-winter (October 2014 – April 2015) and annual (August 2014 – August 2015). Apparent survival (S_A) was defined as:

$$S_A = \frac{\widehat{N}_{t+1}}{\widehat{N}_t}$$

where $\widehat{N}$ is the abundance estimate for a given time period (t). Growth rate for Rainbow Trout was calculated as the difference in length at the end of a time period from the length at the beginning of a time period and recorded as millimeters per month (mm/month) of each time period.

Predator number, used in assessing stream effects on apparent survival and growth, were abundance estimates from the sampling occasion prior to the time period in which apparent survival or growth was being evaluated. I considered predators to be Brown Trout and Brook Trout greater than or equal to 219 mm TL. The 219 mm size threshold was three times the length of an average GR and I used this threshold based on estimates of predator to prey ratios reported in the literature (Parkinson et al. 1989**;** Yule and Luecke 1993; Johnson and Martienz 2000; Ruzycki et al. 2003). Three biomass estimates, predator biomass, competitor biomass, and total biomass (kilograms per hectare), were also calculated from abundance estimates from the sampling occasion prior to the time in which apparent survival or growth was being evaluated. Predator biomass was the biomass of all Brown Trout and Brook Trout greater than or equal to 219 mm TL, competitor biomass was the biomass of all non-predator fish, including Brown Trout and Brook Trout less than 219 mm TL, and total biomass was biomass of all fish in the stream that were not Rainbow Trout.

Prior to constructing statistical models, I examined predictor variable sets for the presence of collinearity (Burnham and Anderson 2002). Variables were removed from inclusion based on how many other predictor variables they were correlated with ($R^2 > 0.5$ and p-value < 0.05) and informed inference based on previous research. Initially, I measured and considered 16 physical and biological predictor variables: strain, stream, stream width, stream flow, stream temperature, stream elevation, stream substrate size (D_{15}, D_{35}, D_{50}, and D_{84}), stream entrenchment, number of predators, predator biomass, total biomass, and competitor biomass. Non-correlated predictor variables were retained in the secondary model sets described below.

To determine if survival, growth rate, and length (mm) differed between the Rainbow Trout strains or among streams, linear regression models were constructed for each time period to test for the effects of each factor considered separately (strain only and stream only), an additive effect of strain and stream, and an intercept-only model. If stream was found to be a contributing factor, I constructed a second model set evaluating the effects of physical and biological stream characteristics. If strain was found to be a contributing factor in the first model set, it was retained as a factor in the second model set. Intercept models as well as models containing singular and additive effects were included in each model set. Akaike's Information Criterion, utilizing second order approximations (AIC_c) was used to rank models. I selected models based on AIC_c differences (Δ AIC_c) and weights (w_i), and I report parameter estimates and associated 95% confidence intervals from the top supported models (Burnham and Anderson 2002).

Laboratory Experiment

Two laboratory experiments were conducted at the Colorado State University Foothills Fisheries Laboratory (FFL) to determine Rainbow Trout fry susceptibility to predation. The first experiment was conducted in September 2014, and the second experiment was conducted in May 2015. The experiment was conducted twice to strengthen my inferences regarding strain-specific susceptibility to predation. The second experiment was also conducted because results from the first experiment suggested that Brown Trout spawning status might have affected predation results. In addition, I added cover as a factor in the second experiment to evaluate if behavioral differences between the Rainbow Trout strains in the presence of cover potentially affected survival.

I used Brown Trout as a predator because lotic ecosystems in Colorado are now dominated by Brown Trout, and Rainbow Trout reintroduction must occur in the presence of Brown Trout. Therefore, it is crucial to understand if there are strain specific differences in survival when faced with Brown Trout predation. Brown Trout were collected from Parvin Lake (Red Feather Lakes, CO) using a boat-mounted electrofishing unit, transferred to the FFL in two oxygenated coolers, and placed into a holding tank. Wild Brown Trout ≥ 250 mm TL were used because they predominantly exhibit piscivorous behavior at this size. Brown Trout averaged 412.7 ± (133.7 SD) g and were an average of 351.4 ± (22.4 SD) mm TL. Rainbow Trout fry used in the experiments averaged 53 ± (1.54 SD) mm TL in 2014 and 72.7 ± (4.06 SD) mm TL in 2015, less than one third the total length of the predators which is the theoretical maximum prey size consumed by salmonid predators (Parkinson et al. 1989; Yule and Luecke 1993; Johnson and Martienz 2000; Ruzycki et al. 2003).

Rainbow Trout were reared at the CPW Bellevue Fish Research Hatchery. To identify the strains during the experiment I tagged each strain using colored Visual Implant Elastomer (VIE). I anesthetized the fish using MS-222 and tagged each fry in the adipose tissue behind the eye, using red for GR and green for GRxCRR. Fry were monitored for mortality for a 24-hour period following tagging. Fish were then transferred to the FFL in two oxygenated coolers and placed into individual large open mesocosm tanks (1,136 L), one for each strain, prior to use in the experiment. Brown Trout were held without food in a separate large open mesocosm tank for 48 hours prior to conducting a trial to ensure that all food eaten previously had been evacuated.

To begin a trial, Brown Trout were placed in large open mesocosms and allowed to acclimate for five minutes. Once acclimated, a 50:50 mix of the GR and GRxCRR of known sizes were stocked into the mesocosms with the Brown Trout. Prior to experimentation in 2014, it was estimated that a single Brown Trout predator (300 g) could consume between 5 and 12 fry in a 24-hour period (40.06 g d^{-1}; Elliott 1975a). Therefore, in the September 2014 experiment, 15 fish each of the GR and GRxCRR were included in a predator arena with a single Brown Trout predator. Trials ran for 24 hours and I completed 12 individual trials. At the end of a trial, all remaining fish in the tank were removed, identified to strain, measured to the nearest millimeter, and weighed to the nearest gram. Brown Trout were only used once and euthanized after being used in a trial. Following experimentation, Brown Trout were sexed to determine if consumption rates varied by sex.

The second experiment was conducted with the same protocols as the first experiment. I added cover as a factor in the second experiment to assess potential differences between the strains in using cover as a refuge from predators. Cover consisted of a PVC box (0.6 m x 0.3 m x 0.9 m) covered with plastic netting (25.4 mm). The mesh size allowed Rainbow Trout fry to enter the box but excluded Brown Trout. Aquarium plants were placed inside the mesh box as an attractant. Trials with and without cover were run simultaneously. I also increased the number of Rainbow Trout in the second experiment to 20 of each strain (40 fish per trial) because in some trials during the first experiment Brown Trout consumed as many as 20 fry.

A linear regression model was constructed for each laboratory experiment to test for the effects of each factor considered separately (strain only, cover only, or sex only), an additive effect of strain and sex (2014 experiment), strain and cover (2105 experiment), and an intercept-only model. Akaike's Information Criterion, utilizing second order approximations (AIC_c) was used to rank models. I selected models based on AIC_c differences (Δ AIC_c) and weights (w_i), and I report parameter estimates and associated 95% confidence intervals from the top supported models (Burnham and Anderson 2002).

RESULTS

Field Experiment

I retained three physical stream characteristics (e.g. average temperature, D_{50}, and entrenchment ratio) and two biological characteristics (predator numbers and competitor biomass) for inclusion in the secondary model selection analyses (Table 2). I began with eleven habitat characteristics and five biological characteristics but eight were removed because they were correlated with other variables in the analyses. All measured substrate sizes were correlated with each other and I chose to retain the median size (D_{50}). Entrenchment was correlated with stream width and depth and I retained it because it more adequately describes the stream connection to the floodplain. I chose to retain average temperature instead of its correlate, elevation, because it directly affects fish physiology. Predator number was used over predator biomass because it more directly measures predation risk as the number of predators capable of consuming the stocked Rainbow Trout. Additionally, my laboratory experiment used individual Brown Trout and not biomass. Total biomass, which included both predator and competitor biomasses was not retained for the same reason. Competitor biomass was retained in the analysis as a measurement of overall competitive effects that the other fish species had on Rainbow Trout fry. Flow was not used because it was only recorded at each sampling event and I did not have any way to calculate flow over the entire study.

At the time of stocking, the GR (72.7 ± 0.6 mm TL) was longer than the GRxCRR (61.4 ± 0.6 mm TL) despite being reared in the hatchery for the same length of time after hatching. The size difference could influence survival because prey size influences the size of predator that could consume the prey. Assuming predators could consume a fish one-third of their length (Parkinson et al. 1989; Yule and Luecke 1993; Johnson and Martienz 2000; Ruzycki et al. 2003), seven of the nine streams had an average predator size that could consume both strains and every stream had predators over 219 mm TL (Figure 2).

Apparent Survival by Strain

The raw data indicated that apparent survival between the strains was not consistent between strains or among the streams. In some streams the apparent survival appeared higher for GR and in others it appeared higher for GRxCRR (Figure 3). Despite the patterns in apparent survival in each stream, model selection results showed that short-term apparent survival did not differ between the strains (ΔAIC_c = 12.38, $w_i \leq 0.002$; Table 3), with an apparent survival of 0.11 [CI = 0.04, 0.17] for the GR and of 0.10 [CI = 0.03, 0.16] for the GRxCRR. The intercept model was ranked highest for both the over-winter and annual time periods and the second best model for these time periods suggested there may be differences in apparent survival between the strains (Table 3). However, the influence of strain in these models was small and the confidence intervals of the β estimates included zero (β = 0.05 [CI = - 0.14, 0.24] and 0.003 [CI = - 0.004, 0.011] for the over-winter and annual time periods, respectively). Over-winter apparent survival of the GR was 0.16 [CI = 0.03, 0.30] and the GRxCRR was 0.21 [CI = 0.08, 0.35]. Annual apparent survival of the GR was 0.005 [CI = 0, 0.01] and the GRxCRR was 0.008 [CI = 0.003, 0.013].

Apparent Survival by Stream

Short-term Rainbow Trout apparent survival differed among the streams short-term two months post stocking (Table 3) and ranged from 0.02 to 0.29 (Figure 4). Results from the AIC_c analysis suggested that apparent survival was most affected by differences in average temperature among the streams (Table 4). In general, average temperature had a positive effect on apparent survival (Figure 5), although the 95% confidence intervals included zero (β_{temp} = 0.060 [CI = - 0.0004, 0.120]). My results also suggest that average pebble size (D_{50}), and entrenchment may have negatively influenced apparent survival (Table 4), but the effects were small, and the associated 95% confidence intervals included zero (β_{D50} = - 0.003 [CI = - 0.009, 0.003]; $\beta_{entrenchment}$ = - 0.006 [CI = -0.021, 0.008]). Apparent survival did not differ by stream in the over-winter or annual survival periods (Table 3).

Growth

Strain and stream had an additive effect on short-term Rainbow Trout growth rate (Table 5). The secondary AIC_c analysis of short-term growth, which included effects of strain and various stream characteristics, indicated that growth differed between the strains. Strain appeared in all of the supported models with a ΔAIC_c less than four (cumulative AIC_c weight = 0.88; Table 6). The GRxCRR exhibited a higher growth rate than the GR, with a difference in growth rate between the two strains of 4.52 ± 1.72 mm/month. Average temperature, which appeared in the top three supported models (cumulative AIC_c weight = 0.75; Table 6), had a positive effect on growth rate across the streams (β_{temp} = 1.55 [CI = 0.56, 2.53]). Overall, growth rate was higher for the GRxCRR than the GR (Figure 6). AIC_c results also suggested that predator numbers had a positive effect and competitor biomass had a negative effect on growth rate (Table 6; Figures 7 and 8); however, the effects of both were small, and the associated 95% confidence intervals were close to zero in their respective models ($\beta_{competitor\ biomass}$ = -0.002 [CI = - 0.003, - 0.0002]; $\beta_{predator\ number}$ = 0.01 [CI = 0.002, 0.03]).

Annual growth rate did not differ by stream (Table 5). Although strain appeared in the second best model of the set (Table 5), the confidence interval of the β estimate included zero (β = 1.802 [- 0.46, 4.06]). Average annual growth rate of the GR (7.38 ± 0.76 mm/month) and GRxCRR (9.18 ± 1.05 mm/month) suggested that a difference in growth between the strains was minor.

Length

Strain and stream had an additive effect on short-term Rainbow Trout length (AIC_c weight = 0.98; Table 7). However, the secondary analysis suggested that strain had little influence on short-term length (Table 8). Strain was only in one of the top models where the ΔAIC_c was less than four (AIC_c weight = 0.1; Table 8). The GR averaged 86.8 ± (0.6 SD) mm TL and the GRxCRR averaged 84.6 ± (0.6 SD) mm TL. Average temperature appeared to influence length among the streams, appearing in the top five models (cumulative AIC_c weight = 0.8; Table 8). In general, average temperature had a positive effect on length (β_{temp} = 3.1 [CI = 1.1, 5.1]; Figure 9). Results also suggested that predator numbers and competitor biomass may also have influenced length (Table 8; Figures 10 and 11), although the effects of both were small, and the associated 95% confidence intervals are close to zero ($\beta_{\text{competitor biomass}}$ = -0.003 [CI = - 0.006, -0.0004]; $\beta_{\text{predator number}}$ = 0.03 [CI = 0.004, 0.05]).

Length did not differ by stream during the over-winter or annual time periods (Table 7). The influence of strain in these models was negligible because confidence intervals of the β estimates included zero (β = - 1.5 [CI = - 43.3, 40.4] and 10.4 [CI = - 16.7, 37.5] for the over-winter and annual time periods, respectively). After one year in the streams, the GR (125.4 ± 22.7 mm TL) was shorter, on average, than the GRxCRR (148.1 ± 32.1 mm TL), although the two did not differ in total length when averaged across the streams.

Laboratory Experiment

The total number of Rainbow Trout consumed in a trial was highly variable in the predation susceptibility experiments, ranging from 0 to 20 fish, and averaging 6 ± 0.3. The intercept model was the top model with the majority of the weight for both the 2014 and 2015 experiments (Table 9), indicating that there was no difference between strains in survival (Figure 12). The model set for the 2014 experiment suggested that male Brown Trout consumed more Rainbow Trout than females ($w_{2014\text{sex}}$ = 0.26), and for the 2015 experiment suggested that treatments with no cover had slightly higher survival ($w_{2015\text{cover type}}$ = 0.30), but all associated 95% confidence intervals included zero ($\beta_{2014\text{sex}}$ = 0.11 [CI = - 0.099, 0.32]; $\beta_{2015\text{cover type}}$ = 0.044 [CI = - 0.023, 0.11]).

DISCUSSION

My primary goal was to evaluate potential differences in survival between the GR and GRxCRR Rainbow Trout strains. Across a wide range of streams in Colorado, apparent survival of age-0 GR was at least as high as the commonly stocked GRxCRR, and laboratory data indicated that survival did not differ between the strains. In addition to apparent survival, annual growth rate and body size did not differ between strains, and both strains recruited into the next age class. I also evaluated potential environmental influences on survival and growth. Apparent survival, growth, and body size differed among streams after the short-term time period, indicating that stream characteristics, particularly average stream temperature, are important determinants of Rainbow Trout performance.

Due to concerns about survival of GR in the wild, they have not been used in wild stocking programs (Schisler et al. 2006); however, their potential to survive in the wild has never been evaluated, particularly for age-0 fish. My study strongly suggests that survival does not differ between the strains and that GR could be used for re-establishment of Rainbow Trout populations in streams and rivers. In contrast, Kopack et al. (2016) showed that the GR had lower survival when stocked as fingerlings (≥ 100 mm TL) into a lake environment. It is difficult to compare my results directly with Kopack et al. (2016), especially due to the differences in systems, but the discrepancy between the studies suggests that further evaluation is warranted. Additionally, my study estimated apparent survival and could not discern between survival and movement from the study area. However, my data clearly show minimal differences in apparent survival and the advantage to stocking GR may outweigh minor differences in survival. The clear advantage of stocking GR would be their high level of resistance and, more importantly, they would not lose resistance due to backcrossing and outcrossing that could occur with the GRxCRR (Schisler et al. 2007; Fetherman et al. 2011; Fetherman et al. 2012). It has been estimated that 9 ± 5 independently segregating genes play a role in GR genetic resistance to *M. cerebralis*, and resistance appears to be additive (Fetherman et al. 2012), suggesting that backcrossing and outcrossing could reduce the number of associated genes working together to increase resistance. Additionally, studies with Chinook Salmon (*Oncorhynchus tshawytscha*) have shown that inbreeding increased infection severity to *M. cerebralis*, indicating that resistance has a genetic component and can lead to potential loss of resistance (Arkush et al. 2002).

No differences in survival were observed during laboratory experiments examining the susceptibility of the strains to Brown Trout predation and these results strengthen the inferences regarding apparent survival in the field. The GR was expected to be more susceptible to predation than the GRxCRR due to its history of domestication and its potential lack of ability to recognize and avoid predators. It has been shown that domestication of as little as one generation can lead to differences in Chinook salmon (*Oncorhynchus tshawytshcha*) fry survival in the presence of Rainbow Trout and Torrent Sculpin (*Cottus rhotheus*) predators (Fritts et al. 2011). Additionally, other studies have demonstrated that hatchery or laboratory-reared fish are more susceptible to predation then their wild counterparts (Suboski and Templeton 1989; Healey and Reinhardt 1991; Berejikian 1995; Shively et al. 1996; Alvarez and Nicieza, 2003). However, the predation susceptibility of GR was similar to GRxCRR for my study, indicating that the GR had similar ability to avoid predation as GRxCRR. Fetherman et al. (2011) showed that the GR and GRxCRR had similar aerobic swimming ability, which may suggest that they may have similar swimming abilities for survival and fitness in the wild (Plaut 2001), although there is no direct evidence linking aerobic swimming performance and survival. My laboratory predator experiment also showed that strain-specific survival did not differ when cover was available, suggesting that cover use is similar between the strains. Similarly, Kopack et al. (2015) showed that the GR exhibited appropriate antipredator behaviors when exposed to a conspecific alarm cue, suggesting that it could inherently sense and respond to danger. Therefore, evidence regarding swimming performance and predator response indirectly supports my observation of no difference in survival in my predator trials.

Although GR typically grow faster and attain larger sizes in the hatchery (Fetherman et. al. 2011), my study indicates that both strains had similar growth and body size in the wild. Interestingly, short-term (August 2014 – October 2015) growth and body size of GRxCRR was twice that of the GR in every study stream, indicating that the cross may be better suited to the natural environment. My short-term growth results are similar to what was seen in Bohlin et al. (2002), where domesticated Brown Trout grew slower than stocked, wild, hatchery-reared Brown Trout. Although I don't know the mechanism causing the short-term growth difference, it is possible that GR consume smaller numbers of natural prey items compared to the GRxCRR. Johnsen and Ugedal (1986, 1989, and 1990) showed that hatchery-reared stocked Brown Trout consumed a lower volume and smaller number of prey items after being stocked compared to wild fish, but this changed after acclimating to the wild environment. Higher growth rate and body size could have ecological implications. Body size is known to influence predation risk, and as body size increases, the number of predators able to consume that prey is reduced (Parkinson et al. 1989; Yule and Luecke 1993; Johnson and Martienz 2000; Ruzycki et al. 2003). In general body size also influences over-winter survival (Hunt, 1969; Smith and Griffith, 1994; Meyer and Griffith 1997) and increased body size is positively related to condition and overwinter survival of Rainbow Trout fry (Meyer and Griffith 1997). I was unable to detect differences in growth and body size after one year due to low numbers of surviving fish. Therefore, I am uncertain if short-term growth differences resulted in long-term consequences for each strain.

My study was not explicitly designed to examine the influence of stream characteristics on survival or growth because I initially selected study streams that were as similar as possible to control for variation in survival due to environmental differences. Although my approach attempted to minimize differences in habitat and environmental characteristics among streams, survival and growth did vary among streams. The variation in growth and survival indicates that environmental characteristics and habitat were important. Strain-specific short-term survival was not predictable, but some streams favored GR while others favored the GRxCRR; therefore, I cannot make inferences about stream environment on strain-specific performance. However, temperature positively influenced overall Rainbow Trout survival. The effect of temperature that I observed is similar to other studies that showed warmer temperatures lead to higher salmonid survival (Hunt, 1969; Smith and Griffith, 1994; Meyer and Griffith, 1997) and higher growth and body size (Austreng et al. 1987; Elliott, 1975c) within the temperature limits that I observed.

Alternatively, studies have also shown that periods of low discharge and warmer water temperatures can negatively affect survival in some rivers (Hicks et al. 1991; Williams et al. 2009).

The short-term, over-winter and annual apparent survival that I observed was relatively similar to other studies for stocked trout fry. Kelly-Quinn and Bracken (1989) showed that survival for stocked Brown Trout fry ranged between 0.115 and 0.37 between the months of June and November. However, my observed short-term apparent survival is considerably less than wild populations, which can range between 70 and 100% (Mitro and Zale 2002). Generally, winter is viewed as the severe time period that regulates population dynamics in animals because of the low survival and variability (e.g. fish: Needham et al. 1945; Willow Tit [*Poecile montanus*]: Lahti et al. 1998; red deer [*Cervus elaphus*] : Albon et al. 2000). The average over-winter survival values I observed was not unrealistic considering annual variation of over-winter survival is common (Needham et al. 1945; Hunt 1969; Seelbach 1993; Ward and Slaney 1993; Quinn and Peterson 1996), and my range of values is similar to the higher values of over-winter survival seen in other Rainbow Trout fry populations (Mitro and Zale 2002). Annual survival for stocked Brown Trout fry in Kelly-Quinn and Bracken (1989) ranged between 0.015 and 0.088 and 0.09 for Mortensen (1977). The annual apparent survival for the GR and the GRxCRR was on the lower range seen by Kelly-Quinn and Bracken (1989). For potential continued persistence to occur within streams stocked by fry, a higher number of fry may need to survive in the short-term time period which occurs in wild populations.

I did not restrict Rainbow Trout movement in my study and therefore could only estimate apparent survival. It is highly likely that that Rainbow Trout moved out of my study and sampling reaches and were not available for capture. Therefore, it is important to consider that the low numbers of fish captured at the end of my study were due to movement as well as mortality and actual survival may be higher than my apparent survival estimates indicate. Hatchery-reared Rainbow Trout have been known to move away from stocking locations (Cresswell 1981; Helfrich and Kendall 1982), and Fetherman et al. (2013) suggested that GR-crosses might move downstream. My uncertainty regarding movement leaves two questions: do stocked Rainbow Trout emigrate from stocking locations and how biased are my apparent survival rates compared to actual survival. I am also interested in the optimal fry stocking number that would maximize retention and survival. A broader sampling and stocking scheme would need to be utilized to answer those questions.

Recruitment of age-0 individuals is critical to reestablish wild Rainbow Trout fisheries because wild Rainbow Trout fry have not survived and recruited into the next age class prior to the use of whirling disease resistant strains within Colorado (Fetherman et al. 2014). With supplementary stocking it may be possible to produce a reproductive population, capable of producing age-0 fish that will continue to survive in the wild in the presence of *M. cerebralis*. However, success will depend on if fish survive to a mature age and begin to reproduce.

My study suggests that stocking pure GR as fry into streams and rivers is a potential alternative to stocking GRxCRR fry. The benefit of stocking the GR over the GRxCRR is that resistance to whirling disease would be maintained if the fish are able to survive to maturity and wild reproduction occurs. However, the higher growth rate of the GRxCRR in the wild stream setting after the short-term was surprising, and may suggest that the GRxCRR may be better suited to the natural environment. Ongoing evaluation of my stocking sites should provide some insight regarding differences in recruitment and reproduction between the strains.

Table 1. Biomass in kilograms per hectare for each stream prior to stocking any Rainbow Trout fry. Brown Trout (*Salmo Trutta*; LOC), Brook Trout (*Salvelinus fontinalis*; BRK), Longnose Sucker (*Catostomus catostomus; LGS*), White Sucker (*Catostomus commersonii; WHS*), Longnose Dace (*Rhinichthys cataractae; LND*), Speckled Dace (*Rhinichthys osculus; SPD*) and Mottled Sculpin (*Cottus bairdii; MTS*), Johnny Darter (*Etheostoma nigrum; JOD*), Brook Stickleback (*Culaea inconstans; BST*), Creek Chub (*Semotilus atromaculatus; CRC*) and Fathead Minnow (*Pimephales promelas; FHM*).

Stream	Average Total Biomass	LOC	BRK	LGS	WHS	LND	SPD	MTS	JOD	BST	CRC	FHM
Lone Pine Creek	3439	2139	0	121	1103	64	0	0	1	10	0	1
N.F. Poudre River	1087	1058	0	0	0	30	0	0	0	0	0	0
Sheep Creek	2079	795	1018	140	0	140	0	0	0	0	0	0
Willow Creek	377	250	32	0	0	0	11	84	0	0	0	0
Spielberg Creek	1622	870	0	235	0	0	94	355	0	0	67	0
Rock Creek	2607	1385	267	955	0	0	0	0	0	0	0	0
Tarryall Creek	2332	2332	0	0	0	0	0	0	0	0	0	0
Michigan Creek	3535	3382	153	0	0	0	0	0	0	0	0	0
Jefferson Creek	7729	7424	0	305	0	0	0	0	0	0	0	0

Table 2. The physical and biological characteristics that were retained and substituted for stream in second AIC_c model analysis.

Stream	Average Temperature (°C)	D50 (mm)	Entrenchment Ratio	Predator Numbers	Competitor Biomass (kg/hectare)
LonePine	13.3	38.4	4.8	147	1390.5
N.F. Poudre	10.6	68.0	10.6	113	758
Sheep	11.5	38.0	4.2	51	1621.3
Willow	9.9	39.6	3.0	58	133.6
Spielberg	11.7	45.4	1.3	132	791.1
Rock	10.1	40.3	15.7	120	2424.8
Tarryall	10.5	45.5	15.0	279	667.4
Michigan	11.3	63.4	2.9	254	2627.8
Jefferson	10.8	67.5	7.8	223	1336

Table 3. Model selection results comparing apparent survival for each time period between strains and among streams. Models with a ΔAIC_c value less than four were considered as contributing information to factors affecting Rainbow Trout apparent survival.

Time Period	Model	logLik	AIC_c	Δ AIC_c	Weight (w_i)
Short-term (2 months)					
	Stream	50.82	-50.20	0	0.998
	Strain + Stream	51.91	-37.83	12.38	0.002
	Intercept	17.97	-31.15	19.06	0
	Strain	18.00	-28.29	21.92	0
Over-winter (6 months)					
	Intercept	4.95	-5.09	0	0.78
	Strain	5.13	-2.54	2.56	0.22
	Stream	13.83	23.77	28.86	0
	Strain + Stream	14.32	37.36	42.46	0
Annual (12 months)					
	Intercept	63.69	-122.58	0	0.71
	Strain	64.26	-120.81	1.77	0.29
	Stream	69.10	-86.77	35.81	0
	Strain + Stream	70.17	-74.35	48.23	0

Table 4. Model selection results for the secondary analysis examining the effects of stream covariates on short-term (two month) post-stocking apparent survival of Rainbow Trout stocked in nine Colorado streams. Models with a ΔAIC_c value less than four were considered as contributing information to covariates affecting Rainbow Trout survival.

Model	logLik	AIC_c	Δ AIC_c	Weight (w_i)
Average Temperature	11.7	-12.6	0	0.41
Intercept	9.1	-12.2	0.43	0.33
D50	9.9	-8.9	3.7	0.063
Entrenchment	9.7	-8.7	4.0	0.055
Competitor Biomass	9.3	-7.8	4.9	0.035
Predator Number	9.1	-7.4	5.2	0.029
Average Temperature + Competitor Biomass	12.6	-7.2	5.5	0.026
Average Temperature + D50	12.4	-6.8	5.9	0.022
Average Temperature + Entrenchment	11.7	-5.5	7.2	0.011
Average Temperature + Predator Number	11.7	-5.5	7.2	0.011
D50 + Entrenchment	10.5	-3.02	9.6	0.0033
D50 + Predator Number	10.2	-2.5	10.2	0.0025
Competitor Biomass + D50	9.9	-1.9	10.7	0.002
Competitor Biomass + Entrenchment	9.8	-1.7	10.9	0
Entrenchment + Predator Number	9.8	-1.7	11	0
Competitor Biomass + Predator Number	9.3	-0.63	12.02	0
Average Temperature + Competitor Biomass + D50	13.1	3.7	16.3	0
Average Temperature + D50 + Predator Number	12.7	4.6	17.2	0
Average Temperature + Competitor Biomass + Predator Number	12.7	4.6	17.3	0
Average Temperature + Competitor Biomass + Entrenchment	12.6	4.8	17.5	0
Average Temperature + D50 + Entrenchment	12.4	5.2	17.8	0
Average Temperature + Entrenchment + Predator Number	11.8	6.5	19.1	0
D50 + Entrenchment + Predator Number	11.4	7.1	19.6	0
Competitor Biomass + D50 + Entrenchment	10.6	8.8	21.5	0
Competitor Biomass + D50 + Predator Number	10.5	9.1	21.7	0
Competitor Biomass + Entrenchment + Predator Number	10	9.9	22.6	0
Average Temperature + Competitor Biomass + D50 + Predator Number	13.8	26.4	39.01	0
Average Temperature + Competitor Biomass + Entrenchment	13.1	27.7	40.3	0
Average Temperature + D50 + Entrenchment + Predator Number	12.9	28.2	40.3	0
Average Temperature + Competitor Biomass + Entrenchment + Predator Number	12.7	28.6	41.3	0
Competitor Biomass + D50 + Entrenchment + Predator Number	11.7	30.6	43.2	0
Average Temperature + Competitor Biomass + D50 + Entrenchment + Predator Number	13.9	98.2	111.0	0

Table 5. Model selection results examining the effects of strain and stream as factors thought to affect the growth (mm/month) of Rainbow Trout stocked in nine Colorado streams. Models with a ΔAIC_c value less than four were considered as contributing information to factors affecting Rainbow Trout growth.

Time Period	Model	logLik	AIC_c	Δ AIC_c	Weight (w_i)
Short-term					
	Strain + Stream	-5.87	77.75	0	0.999
	Strain	-42.05	91.82	14.07	0.001
	Intercept	-47.42	99.63	21.87	0
	Stream	-40.40	132.24	54.49	0
Over-Winter					
Annual					
	Intercept	-32.30	69.61	0	0.51
	Strain	-30.76	69.71	0.097	0.49
	Stream	-25.19	104.79	34.77	0
	Strain + Stream	-18.39	111.79	42.18	0

Table 6. Model selection results for the secondary analysis examining the effects of stream covariates thought to affect the short-term (two month) post-stocking growth rate (mm/month) of Rainbow Trout stocked in nine Colorado streams. Models with a ΔAIC_c value less than four were considered as contributing information to covariates affecting Rainbow Trout growth rate.

Model	logLik	AIC_c	$\Delta\ AIC_c$	Weight (w_i)
Strain + Average Temperature + Competitor Biomass + Predator Number	-33.8	87.32	0	0.44
Strain + Average Temperature	-39.0	89.08	1.8	0.18
Strain + Average Temperature + Predator Number	-37.4	89.71	2.4	0.13
Strain + Average Temperature + Competitor Biomass	-37.4	89.76	2.4	0.13
Strain	-42.1	91.82	4.5	0.05
Strain + Predator Number	-40.8	92.71	5.4	0.03
Strain + Competitor Biomass	-41.5	94.08	6.8	0.015
Strain + Competitor Biomass + Predator Number	-39.5	94.08	6.8	0.015
Average Temperature	-45.9	99.44	12.1	0.001
Intercept	-47.4	99.63	12.3	0.001
Predator Number	-46.8	101.2	13.9	0.0004
Average Temperature + Predator Number	-45.1	101.3	14.01	0.0004
Average Temperature + Competitor Biomass	-45.1	101.4	14.04	0.0004
Competitor Biomass	-47.1	101.9	14.6	0.0003
Average Temperature + Competitor Biomass + Predator Number	-43.8	102.6	15.3	0.0002
Competitor Biomass + Predator Number	-46.1	103.3	16.0	0.0001

Table 7. Model selection results examining the effects of strain and stream as factors thought to affect the length (mm) of Rainbow Trout stocked in nine Colorado streams. Models with a ΔAIC_c value less than four were considered as contributing information to factors affecting Rainbow Trout length

Time Period	Model	logLik	AIC_c	Δ AIC_c	Weight (w_i)
Short-term					
	Strain + Stream	-18.35	102.70	0	0.98
	Stream	-30.01	111.44	8.75	0.012
	Intercept	-54.95	114.69	11.99	0
	Strain	-54.53	116.77	54.49	0
Over-winter					
	Intercept	-52.53	110.16	0	0.83
	Strain	-52.47	113.35	3.19	0.17
	Stream	-38.67	122.14	11.99	0
	Strain + Stream	-38.24	139.48	29.33	0
Annual					
	Intercept	-68.42	141.84	0	0.77
	Strain	-68.04	144.25	2.41	0.23
	Stream	-58.43	170.85	29.01	0
	Strain + Stream	-55.67	186.34	44.49	0

Table 8. Model selection results for the secondary analysis examining the effects of stream covariates thought to affect the short-term (two month) post-stocking length (mm) of Rainbow Trout stocked in nine Colorado streams. Models with a ΔAIC_c value less than four were considered as contributing information to covariates affecting Rainbow Trout length.

Model	logLik	AIC_c	ΔAIC_c	Weight (w_i)
Average Temperature + Competitor Biomass +Predator Number	-47.3	109.7	0	0.37
Average Temperature	-52.1	111.8	2.2	0.12
Average Temperature + Predator Number	-50.5	112.1	2.5	0.11
Average Temperature+ Competitor Biomass	-50.6	112.2	2.5	0.10
Strain + Average Temperature + Competitor Biomass + Predator Number	-46.3	112.3	2.6	0.10
Strain + Average Temperature	-51.5	114.0	4.4	0.041
Strain + Average Temperature + Predator Number	-49.8	114.7	4.9	0.03
Intercept	-54.9	114.7	5.0	0.03
Strain + Average Temperature + Competitor Biomass	-49.9	114.7	5.1	0.03
Predator Number	-53.8	115.3	5.6	0.02
Competitor Biomass + Predator Number	-52.6	116.2	6.6	0.01
Competitor Biomass	-54.4	116.6	6.9	0.01
Strain	-54.5	116.8	7.1	0.01
Strain + Predator Number	-53.3	117.7	8.0	0.007
Strain + Competitor Biomass	-54	119.0	9.4	0.003
Strain + Competitor Biomass + Predator Number	-52	119.0	9.4	0.003

Table 9. Model selection results for the 2014 and 2015 laboratory experiment. Strain and sex were main factors analyzed in 2014. Strain and cover type were the factors analyzed in 2015. Models with a ΔAIC_c value less than four were considered as contributing information to factors affecting Rainbow Trout survival.

Year	Model	logLik	AIC_c	$\Delta\ AIC_c$	Weight (w_i)
2014					
	Intercept	0.451	3.67	0	0.53
	Sex	1.08	5.05	1.4	0.26
	Strain	0.478	6.24	2.6	0.15
	Strain + Sex	1.11	7.9	4.2	0.06
2015					
	Intercept	36.4	-68.5	0	0.38
	Cover Type	37.3	-68.1	0.46	0.30
	Strain	36.8	-67.0	1.5	0.18
	Strain + Cover Type	37.7	-66.5	2.0	0.14

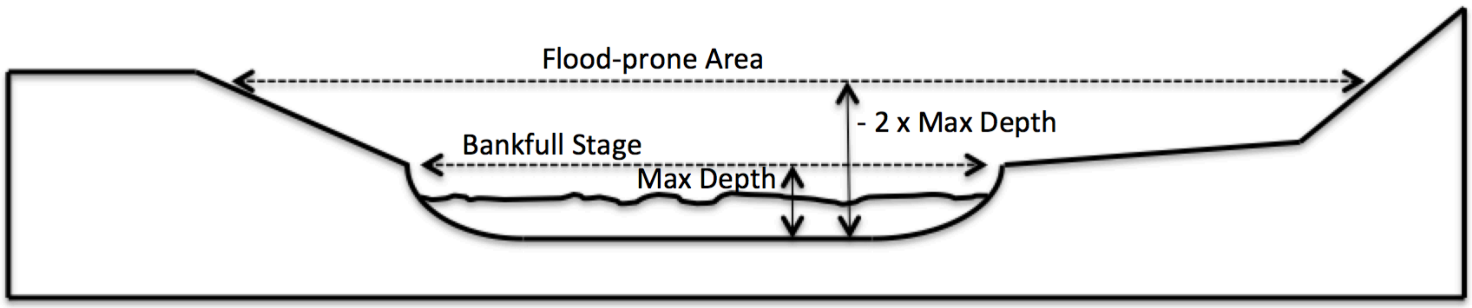

Figure 1. A cross section of a stream showing bankfull stage and maximum depth of the stream. The flood-prone area is the width of the floodplain at twice the maximum stream depth. Entrenchment ratio was calculated by dividing the width of the flood-prone area by the width of the banfull stage.

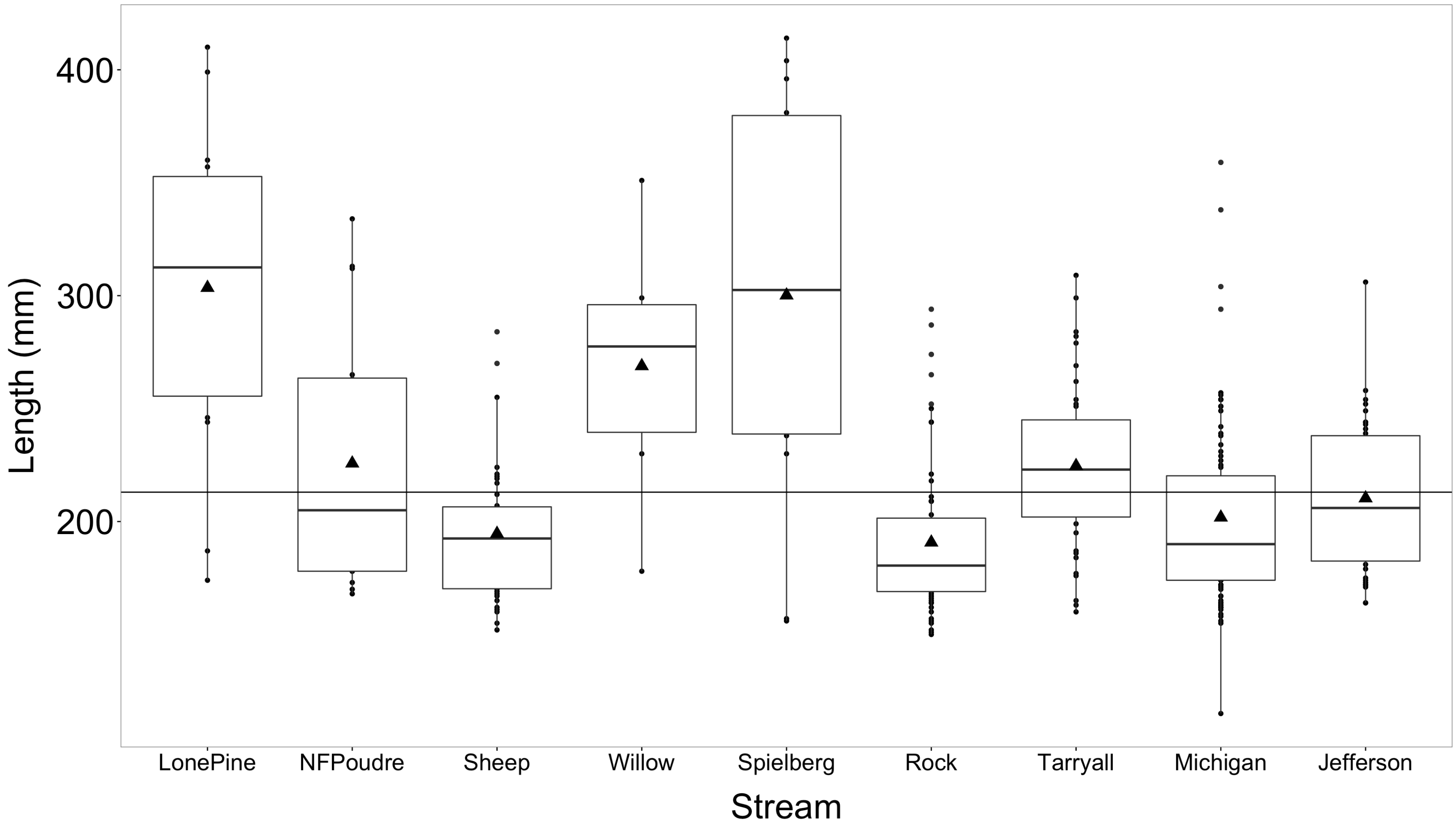

Figure 2. Adult salmonid (Brown Trout and Brook Trout) lengths within each stream prior to stocking. Sold black triangle denotes the average predator length and the solid black line denotes the length three times the GR length.

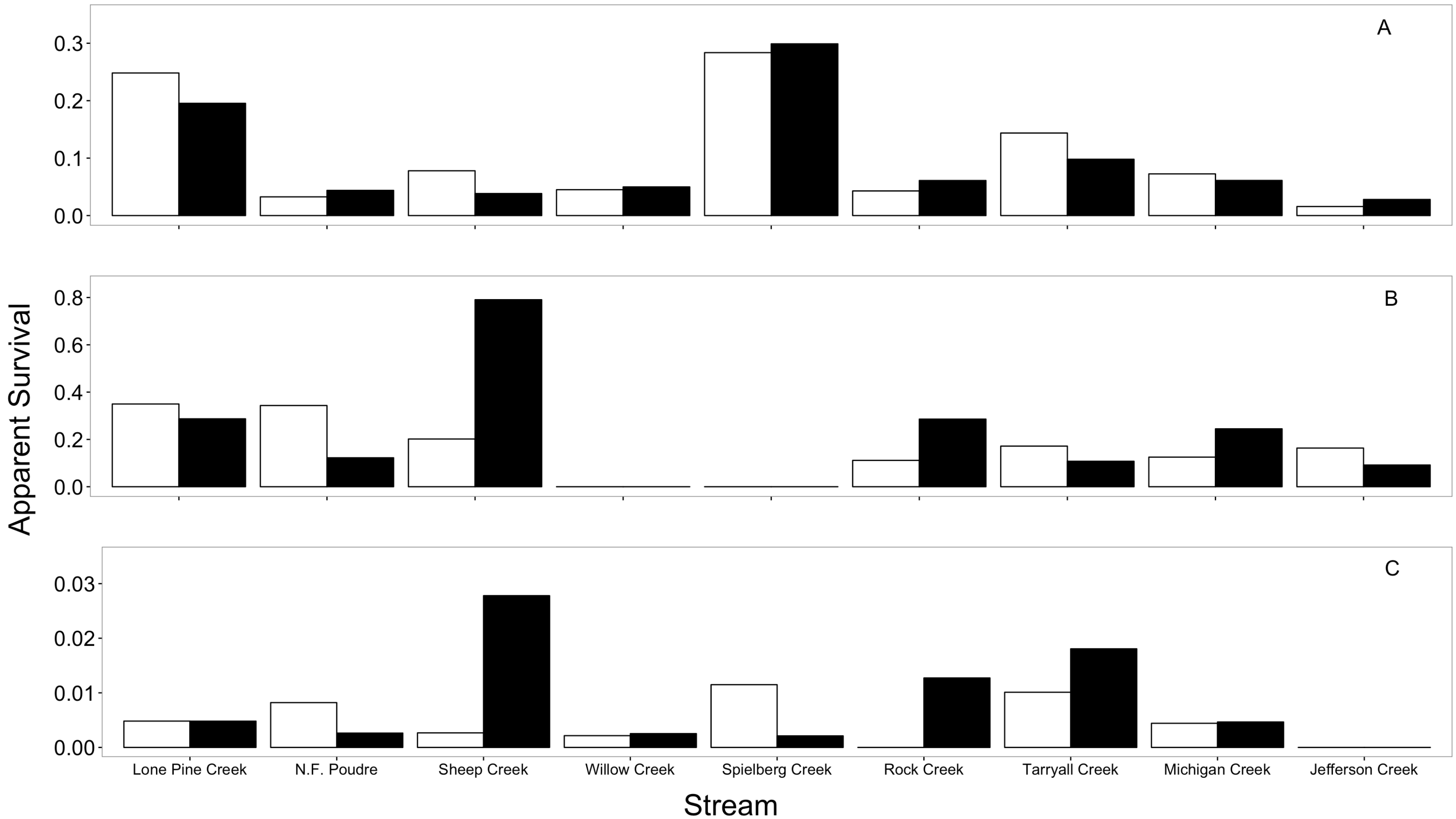

Figure 3. Apparent survival for each strain within each stream at short-term (August 2014 – October 2014; A), over-winter (October 2014 – April 2015; B), and annual (August 2014 – August 2015; C) time periods. White bars represent GR and black bars represent GRxCRR. Willow Creek and Spielberg Creek were not sampled over-winter due to hazardous access and unsafe sampling conditions. Note that the y-axis is different between the panels to better show differences in apparent survival between the strains.

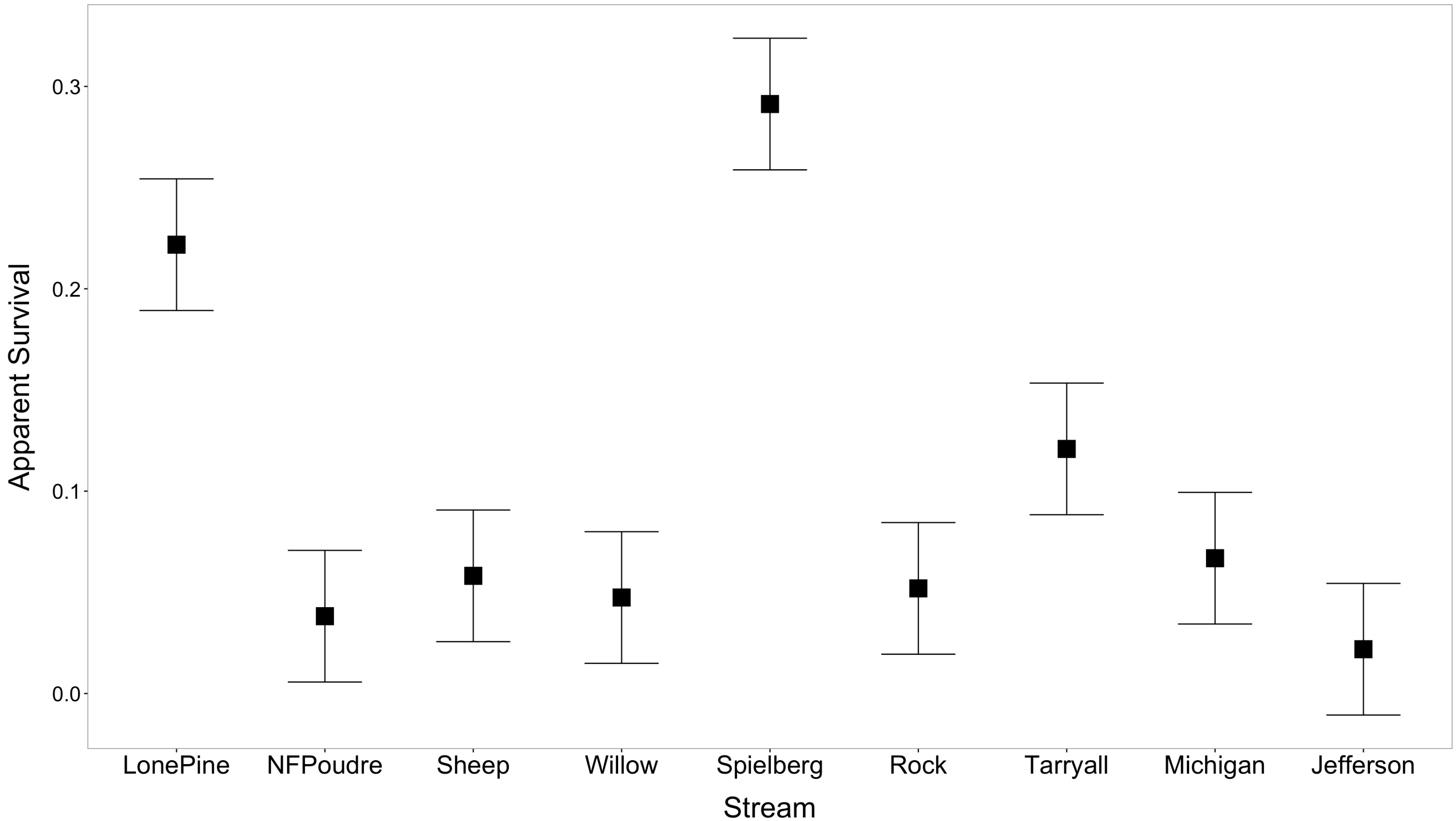

Figure 4. Average apparent survival by stream for the short-term time period (August 2014 – October 2014). Black squares represent apparent survival for each of the nine streams. Vertical bars represent the 95% confidence intervals.

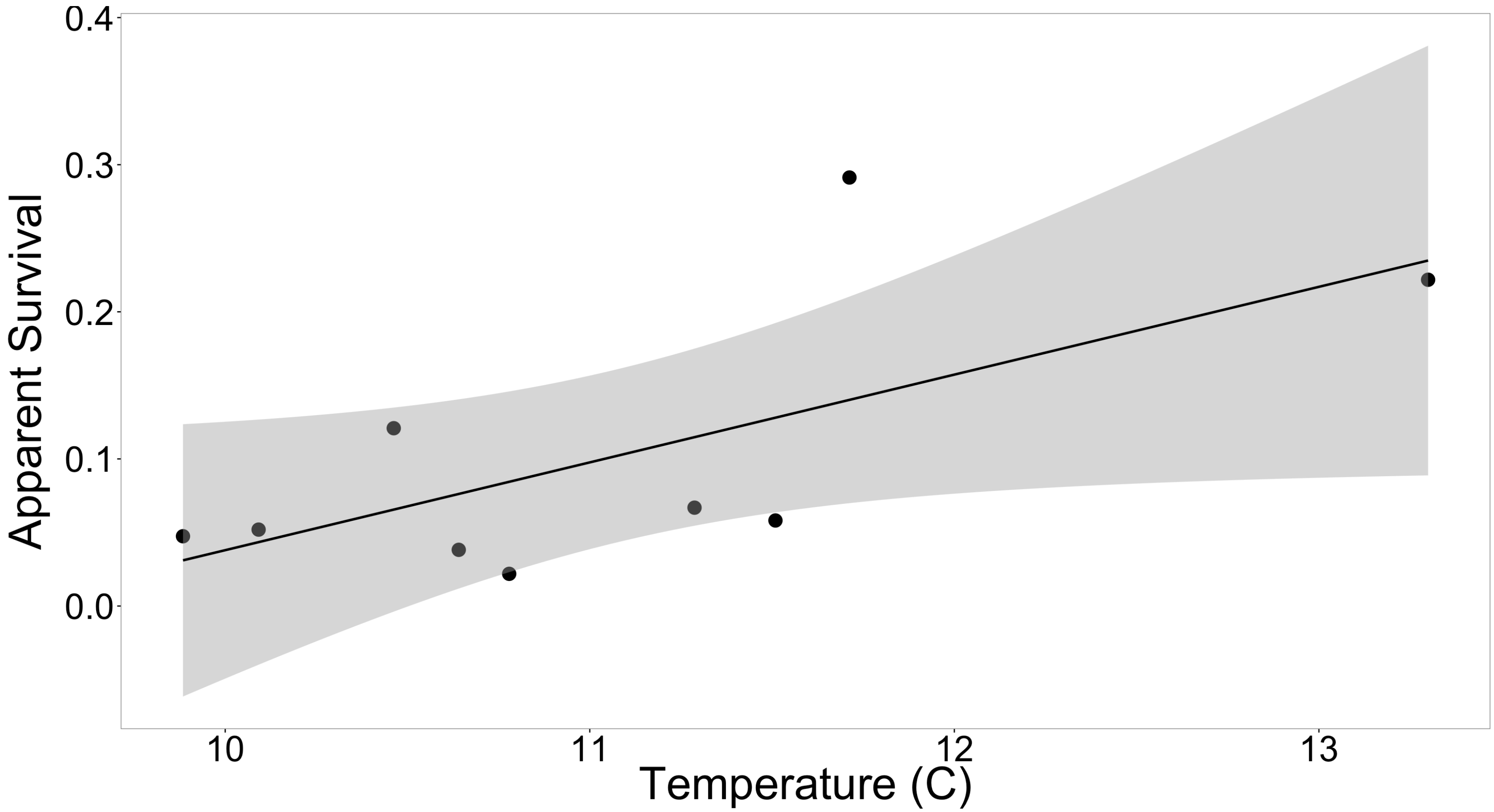

Figure 5. Relationship between average stream temperature (°C) and Rainbow Trout average apparent survival two months post stocking as fry. Dots represent the average survival and average temperature for each of the nine streams. The gray shaded area represents the 95% confidence interval for the trend line describing the data points.

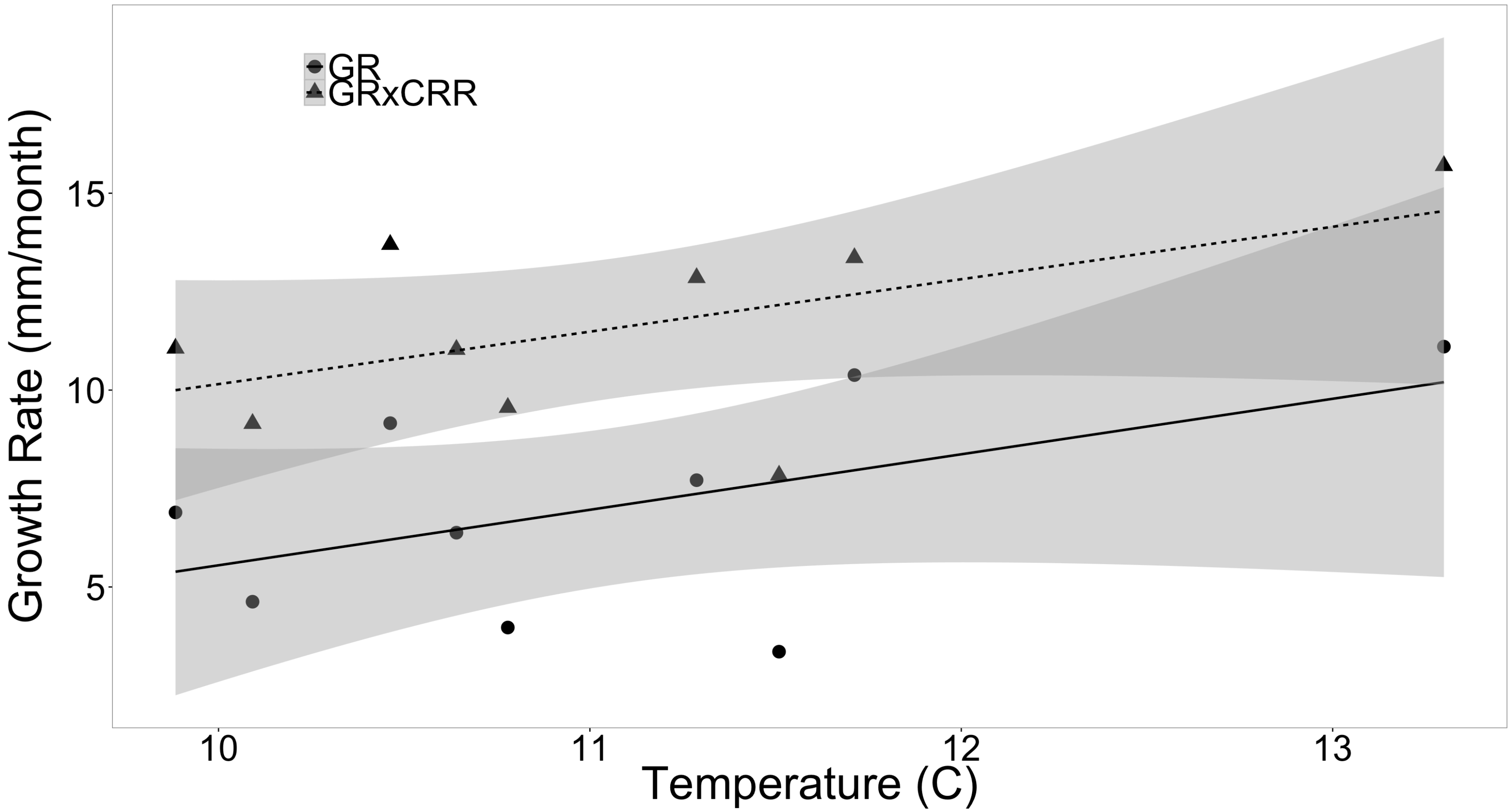

Figure 6. Predicted growth rates compared to average stream temperature (°C) for GR (circles; solid line) and GRxCRR (triangles; dotted line) two months post stocking as fry. The gray shaded areas represent the 95% confidence intervals for the trend lines describing the data points.

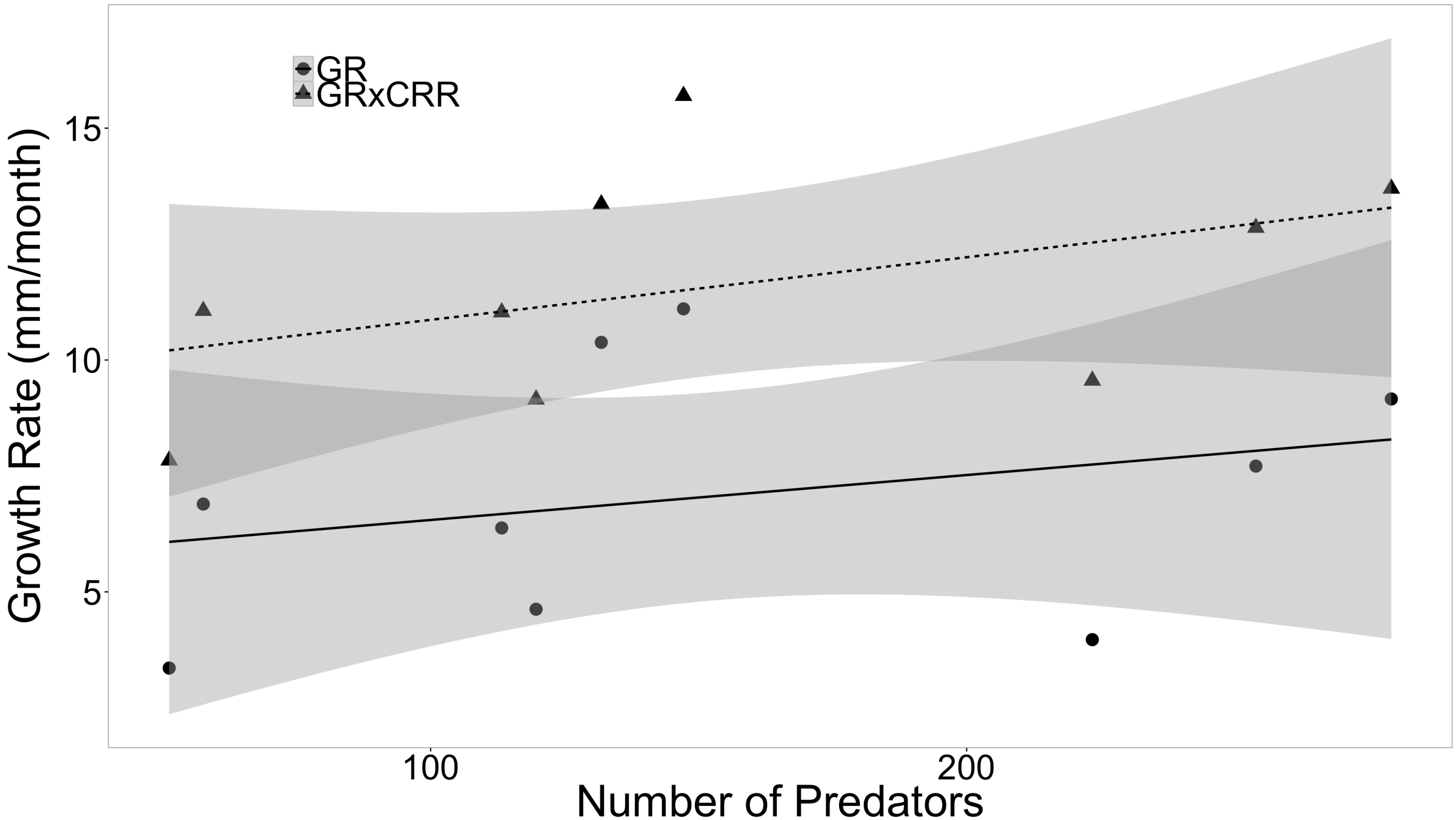

Figure 7. Predicted growth rates compared to predator numbers for GR (circles; solid line) and GRxCRR (triangles; dotted line) two months post stocking as fry. The gray shaded areas represent the 95% confidence intervals for the trend lines describing the data points.

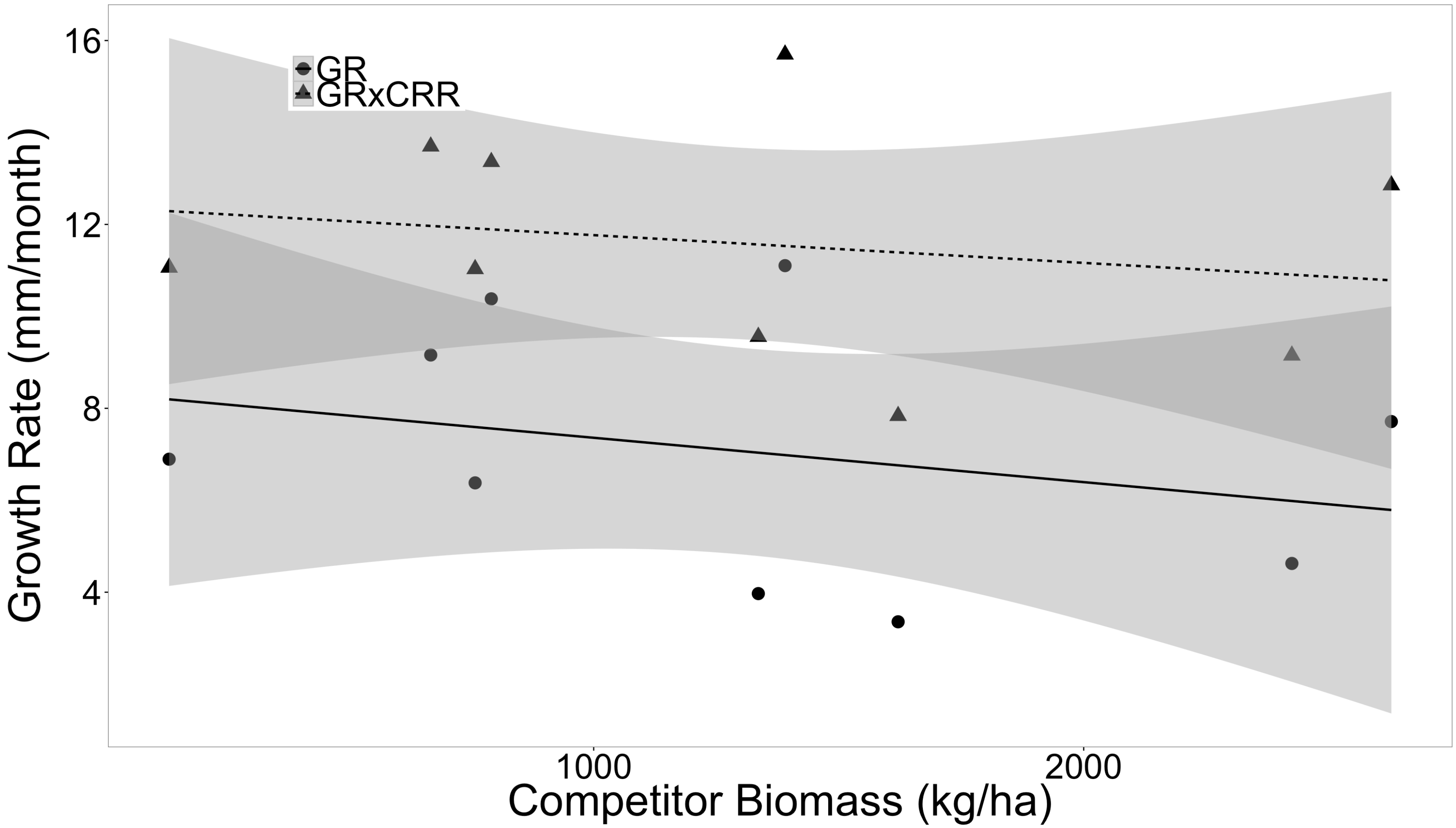

Figure 8. Predicted growth rates compared to competitor biomass for GR (circles; solid line) and GRxCRR (triangles; dotted line) two months post stocking as fry. The gray shaded areas represent the 95% confidence intervals for the trend lines describing the data points.

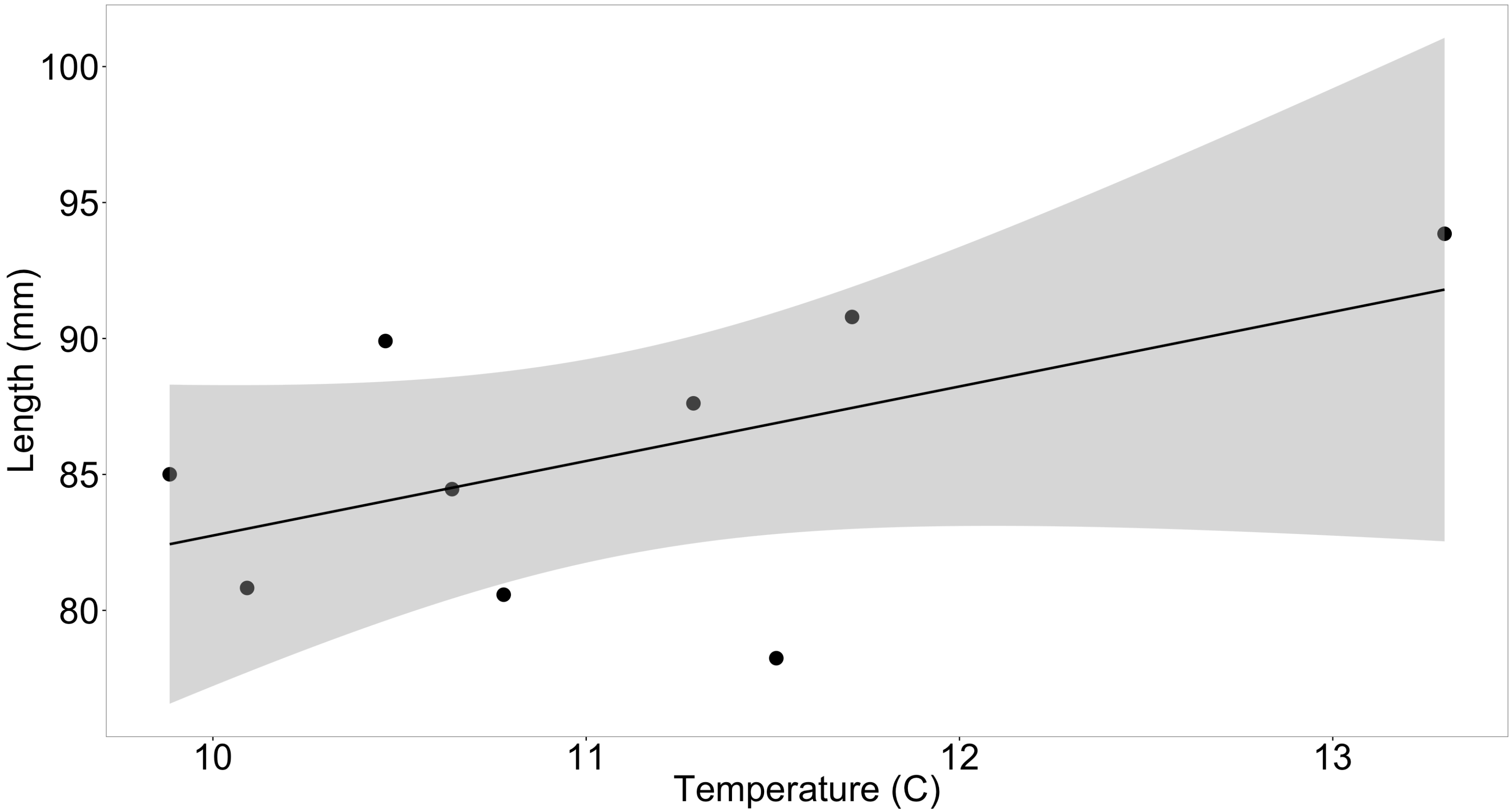

Figure 9. Comparison of Rainbow Trout lengths to average stream temperature (°C) after the short-term time period. The gray shaded area represents the 95% confidence interval for the trend line describing the data points.

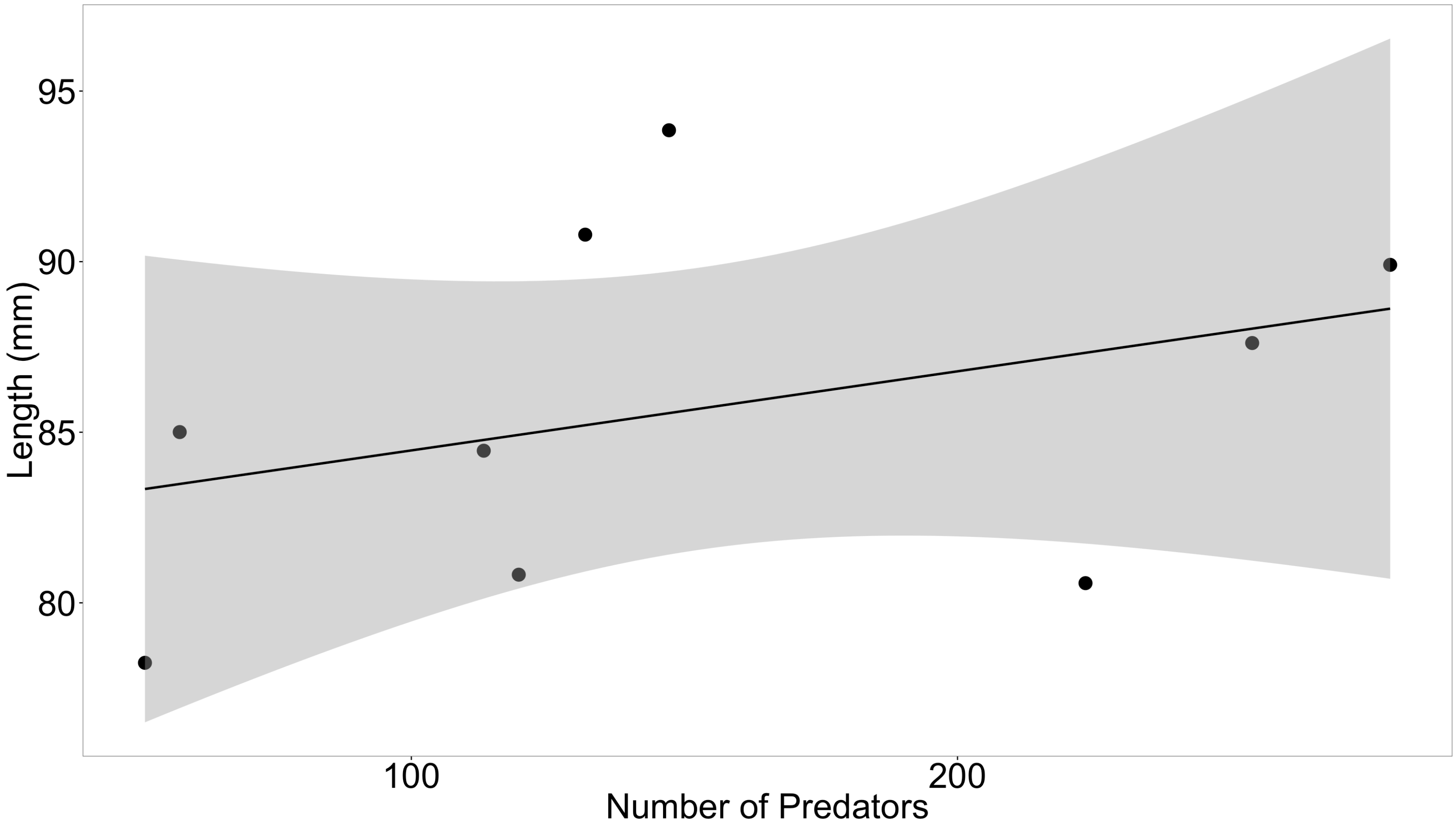

Figure 10. Lengths of Rainbow Trout fry with respect to number of predators after the short-term time period. The gray shaded area represents the 95% confidence interval for the trend line describing the data points

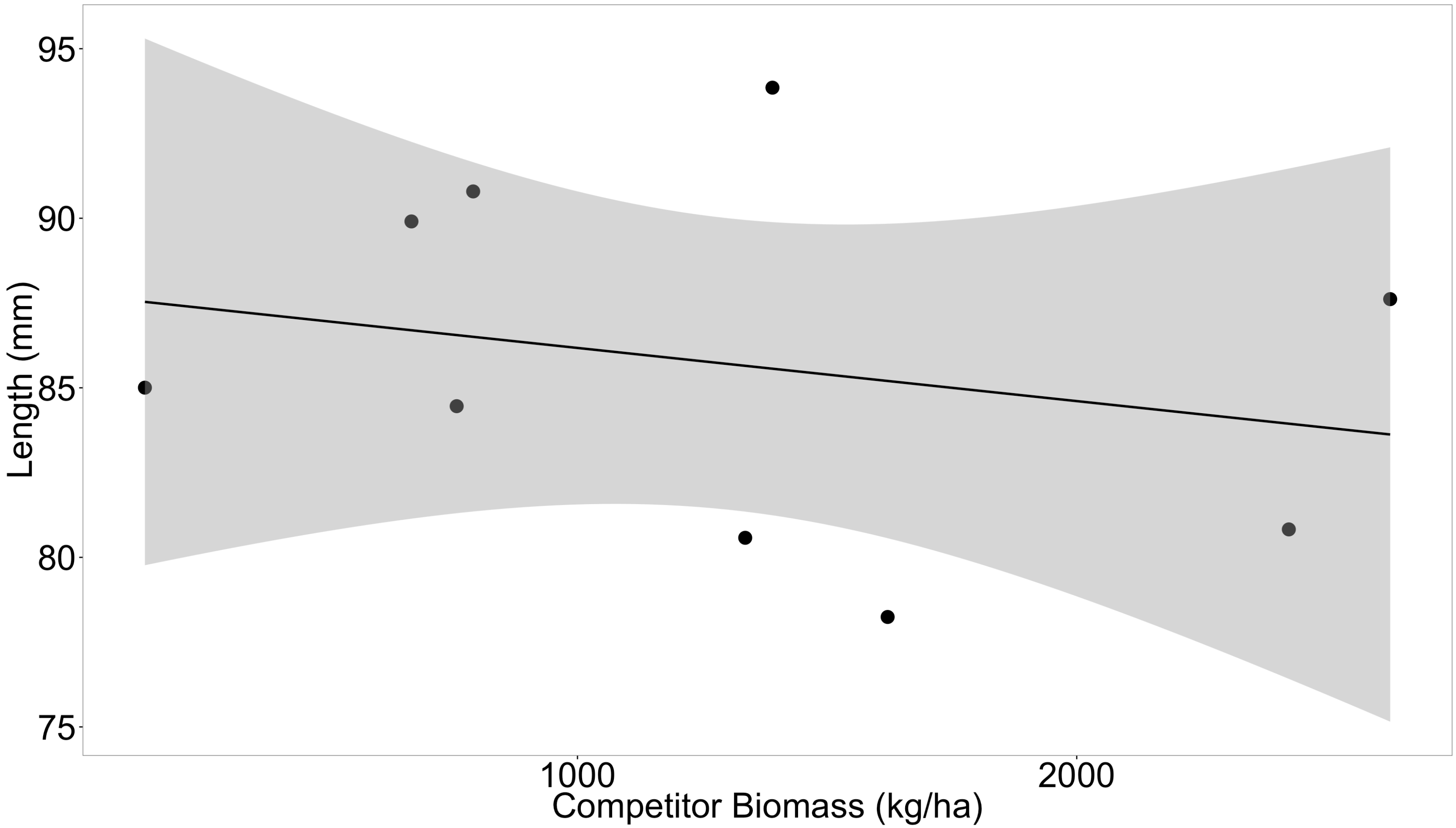

Figure 11. Lengths of Rainbow Trout fry with respect to competitor biomass after the short-term time period. The gray shaded area represents the 95% confidence interval for the trend line describing the data points

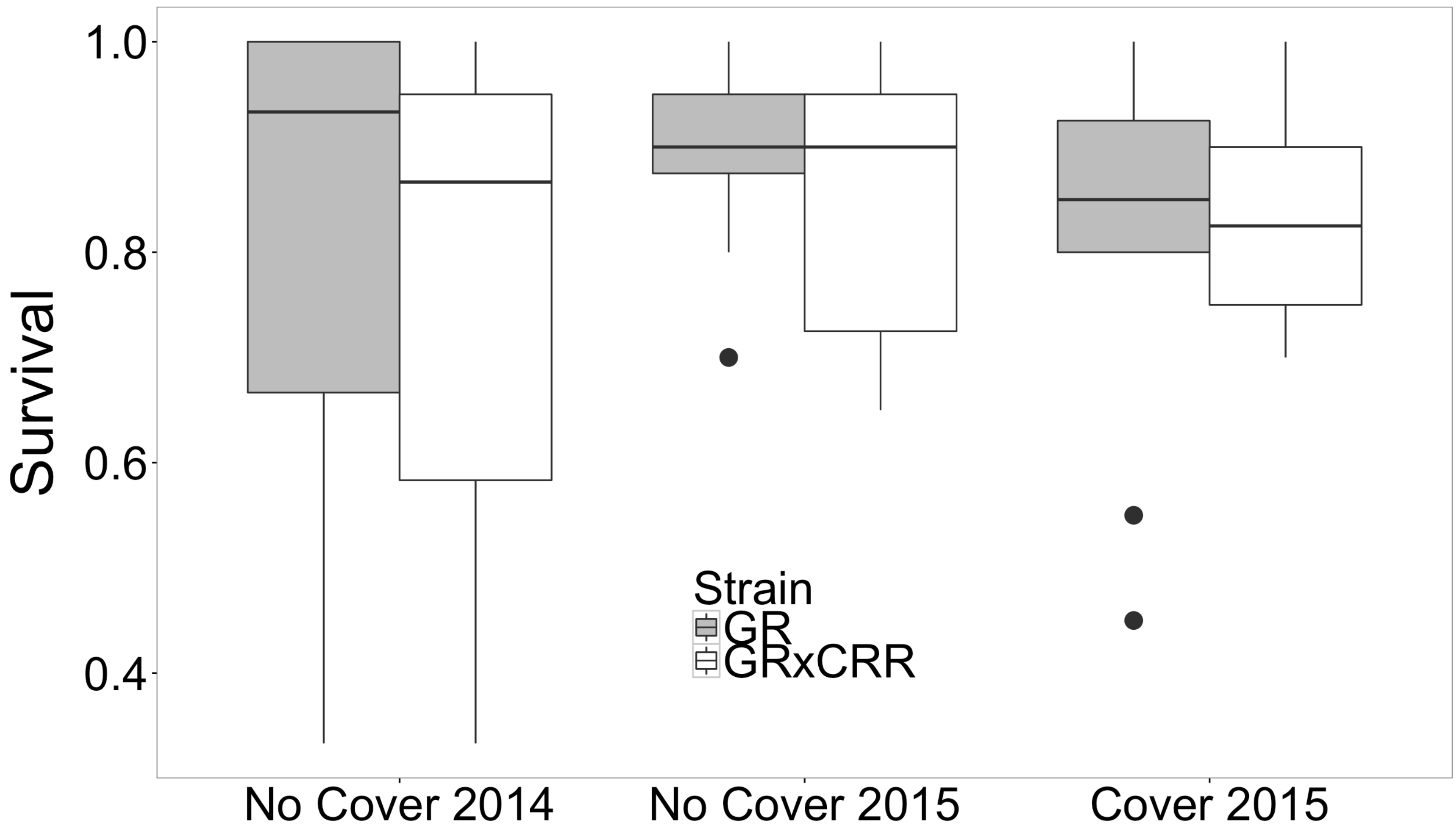

Figure 12. Twenty four-hour survival between GR and GRxCRR with no cover and cover when stocked with an individual Brown Trout in 2014 and 2015.

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