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MANAGEMENT BRIEF

Biotic and Abiotic Factors Affecting Short-Term Survival of Two Age-0 Rainbow Trout Strains in Colorado Streams

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Abstract

Both biotic and abiotic factors can influence the survival and growth of age-0 salmonids. Diseases, such as whirling disease, can also affect salmonid demographics and population dynamics. Here, we conducted a supplementary analysis and evaluated specific stream characteristics that may have been responsible for the differences in growth and survival of two whirling disease resistant Rainbow Trout Oncorhynchus mykiss strains observed by Avila et al. (2018). We used regression modeling to analyze the influence of the biotic and abiotic characteristics of nine streams on the short-term apparent survival and growth of two Rainbow Trout strains, 5,000 German Rainbow Trout and 5,000 German Rainbow Trout × Colorado River Rainbow Trout in each stream. Akaike's information criterion (AIC_c) model selection was used to identify the factors that most affected short-term survival and growth. Average stream temperature had the largest (positive) effect, $\beta_{temp} = 0.060$, on short-term survival. Rainbow Trout strain, average stream temperature (β_{temp} = 1.55), competitor biomass ($\beta_{competitor\ biomass} = -0.002$), and predator number ($\beta_{predator\ number} = 0.01$) additively affected short-term growth. Our results indicate that both biotic and abiotic factors are important short-term determinants of Rainbow Trout poststocking performance and may account for the differences in survival and growth that we observed among stocking locations.

Biotic and abiotic factors both play an important role for survival and growth of juvenile/age-0 trout and salmon and warrant consideration when assessing critical vital rates while reestablishing populations. Biotic factors such as the number or density of predators and competitors or disease can influence growth and survival of salmonids (Fausch 1984; Nehring and Walker 1996; Fetherman et al. 2014; Hasegawa 2016). Diseases, especially those that have become established in a system and are unlikely to be eradicated, can play a large role in affecting salmonid vital rates and population dynamics.

Population declines of Rainbow Trout *Oncorhynchus mykiss* in Colorado have been linked to loss of recruitment and reduced survival of age-0 fish due to whirling disease (Nehring and Walker 1996; Fetherman et al. 2014). Whirling disease, caused by the parasite *Myxobolus cerebralis*, has been a major factor in Rainbow Trout population declines in the Rocky Mountain region of North America (Nehring and Walker 1996; Vincent 1996; James et al. 2021), specifically Colorado where persistence of the

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parasite continues to affect Rainbow Trout management (Fetherman et al. 2014).

Management of M. cerebralis in the wild is difficult, particularly in locations where environmental conditions, such as low flows and fine sediment accumulation (Zendt and Bergersen 2000), perpetuate the abundance of the intermediate Tubifex tubifex host. However, one option undertaken by the state of Colorado is to use M. cerebralis-resistant Rainbow Trout to break the parasite life cycle and reduce parasite loads in the wild (Fetherman et al. 2014). In more recent years, stocking fry (<50 mm TL) has been used as a strategy for stocking M. cerebralis-resistant Rainbow Trout (Avila et al. 2018; Fetherman and Avila 2021). Not only can interactions between the environment and disease affect survival of the fry, but other environmental variables may also influence the survival of stocked fish. It is well known that abiotic habitat variables, such as temperature, water quality, and substrate, influence salmonid growth and survival (Meyer and Griffith 1997: Rosenfeld and Boss 2001: Ebersole et al. 2006; Pess et al. 2011). Additionally, factors such as mean substrate, velocity, and depth have been shown to be important determinants of the number of Rainbow Trout fry in a given location, and stocking, interspecific competition, and disease affect habitat associations of salmonid fry (Fetherman and Avila 2021).

In this study, we expanded on Avila et al. (2018), who completed a replicated field experiment to assess differences in apparent survival and growth among two whirlingdisease-resistant Rainbow Trout (Schisler et al. 2006; Fetherman et al. 2011, 2012) strains were stocked as fry in nine streams, the majority in which Myxobolus cerebralis is now endemic (Avila et al. 2018). Our original study found that short-term apparent survival differed by stream and growth rate differed by both strain and stream. The individual streams influenced apparent survival and growth of the stocked Rainbow Trout despite the selection of streams that were qualitatively similar with respect to stream size, elevation, and predator and competitor dynamics. Here, we conducted a supplementary analysis to evaluate the effects of the biotic and abiotic habitat data collected in the nine streams in Avila et al. (2018), including average temperature, competitor biomass, pebble size, entrenchment ratio, and predator numbers, on short-term apparent survival and growth of two M. cerebralis-resistant strains of Rainbow Trout.

METHODS

A detailed description of each stream, including location, name, fish species present, and stocking and fish sampling protocols can be found in Avila et al. (2018). Briefly, stream habitat evaluations and fish sampling were conducted in nine streams across Colorado located around Red Feather Lakes, Colorado (n = 3); Kremling, Colorado (n = 3); and Jefferson,

Colorado (n = 3) between July 2014 and August 2015. Two strains of Rainbow Trout were reared at the Colorado Parks and Wildlife Rifle Falls Fish Hatchery for the same amount of time and stocked into each stream (5,000 German Rainbow Trout [GR] and 5,000 GR × Colorado River Rainbow Trout [CRR] per stream) in August 2014. At the time of stocking the GR × CRR $(61.4 \pm 0.6 \,\mathrm{mm} \,\mathrm{TL} \,\mathrm{[mean} \pm \mathrm{SD]})$ were slightly smaller than the GR $(72.7 \pm 0.6 \,\mathrm{mm} \,\mathrm{TL})$; Avila et al. 2018). The strains were identified by the presence or absence of Northwest Marine Technology coded wire tags. Each stream was visited once to establish sampling sites prior to stocking and three times after stocking to evaluate short-term (2 months), over winter (6 months), and year one (12 months) apparent survival (fish movement was not constricted; Avila et al. 2018), and growth rates. Three-pass removal was conducted by backpack electrofishing to estimate abundance of all fish species located within each site (two per stream) on each visit.

We selected streams based on accessibility for stocking. fish community structure, and a visual qualitative assessment of habitat, attempting to select streams of similar size and with similar physical characteristics (Avila et al. 2018). However, during the original study, we understood that the initial visual assessment was qualitative and chose to measure a suite of stream habitat characteristics to quantify potential differences among streams. Habitat measurements were made after each sampling event in October 2014, April 2015, and August 2015. Starting at the downstream border of each sampling site, width, depth, and flow measurements were made along transects at 0, 25, 50, 75, and 100% of the total sample site length (average site length 66 m; Avila et al. 2018). Depth and flow were measured perpendicular to the flow and 10 depth and flow measurements were taken at equally spaced intervals across the channel at each transect. Width and depth was recorded to the nearest centimeter, and flow (m/s) 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 downstream border of each sampling site.

We also measured temperature, dominant substrate particle size, and entrenchment ratio because these metrics have been correlated with fish survival and growth (Pepin 1991; Selong et al. 2001; Suttle et al. 2004; Mazeika et al. 2006). Temperature was measured every 244 min from the beginning to the end of the study, using Maxim Integrated iButton temperature loggers placed in or near each sampling site at the time of fry stocking. The 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. The collected temperature values were used to construct average temperature for the sampling sites for the period investigated within the analysis (September 2014–October 2014). Measurements of

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entrenchment ratio (width of the flood-prone area divided by width of the bankfull stage) and representative pebble counts were collected at every sampling site during August 2015. Entrenchment ratio was measured using a method adapted from Rosgen (1996). A modified pebble count protocol was used by stratifying the length of the sampling station into 0, 25, 50, 75, and 100% transects of the sample site length. The width of 20 rocks was measured along their intermediate axis at evenly spaced intervals along each transect for a total of 100 rock width measurements made 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 percentage of smaller-than-size values (D_{15} , D_{35} , D_{50} , and D_{84}) for each sampling site.

Estimated predator abundance during the prior period (July 2014-August 2014) was used for the current period (September 2014–October 2014) in which apparent survival or growth rate was being evaluated because it was assumed that predator abundance during the prior period would affect fish in the estimate at the beginning of the current period. We considered predators to be Brown Trout and Brook Trout ≥219 mm TL. The 219-mm size threshold was based on the gape limit of predators being three times the length of an average GR at stocking, and we used this threshold based on estimates of predator to prey size ratios reported in the literature (Parkinson et al. 1989; Yule and Luecke 1993; Johnson and Martinez 2000; Ruzycki et al. 2003; Avila et al. 2018). 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 Salmo trutta and Brook Trout Salvelinus fontinalis ≥219 mm TL, competitor biomass was the biomass of all nonpredatory fish (Longnose Sucker Catostomus catostomus, White Sucker Catostomus commersonii, Longnose Dace Rhinichthys cataractae, Speckled Dace Rhinichthys osculus, Mottled Sculpin Cottus bairdii, Johnny Darter Etheostoma nigrum, Brook Stickleback Culaea inconstans, Creek Chub Semotilus atromaculatus, and Fathead Minnow Pimephales promelas; Avila et al. 2018) found within the same sampled habitats with the Rainbow Trout (including Brown Trout and Brook Trout <219 mm TL), and total biomass was biomass of all fish in the stream that were not Rainbow Trout.

Prior to constructing regression models, we examined the predictor variable set for the presence of collinearity (Burnham and Anderson 2002; Dormann et al. 2013). Predictor variables were removed from inclusion based on correlations with other variables (coefficient of determination $[R^2] > 0.5$ and P < 0.05), and choices between two collinear variables were informed by previous research and professional

judgment and are described in the results (Burnham and Anderson 2002). Initially, we considered 16 biotic and abiotic 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 ratio, number of predators, predator biomass, total biomass, and competitor biomass. Noncorrelated predictor variables were retained in the model sets described below.

After assessing collinearity, we retained three abiotic stream characteristics (average temperature, stream substrate D_{50} , and entrenchment ratio) and two biotic characteristics (predator numbers and competitor biomass). All substrate sizes were correlated with each other, and we retained the median size (D_{50}) . Entrenchment ratio was correlated with stream width and depth, and we retained entrenchment ratio because it more adequately describes the stream connection to the floodplain. We retained average temperature instead of elevation because it more directly affects fish physiology. Predator number was used instead of predator biomass because it more directly measures predation risk as the number of predators capable of consuming stocked Rainbow Trout fry. Competitor biomass was retained as a measurement of overall competitive effects that other fish species had on Rainbow Trout fry. Although initially thought to be an important predictor variable, flow was not used because it was only recorded during each sampling event and was not calculated over the entire study; flow events occurring between measurements were thought to more likely affect survival or growth than the flows measured at the time of sampling.

Our previous Akaike's information criterion (AIC_c) analysis showed that the response variable of apparent survival during the short-term (2-month) period differed among streams and the response variable of growth differed between the strains and among streams (Avila et al. 2018). Estimated average short-term survival was 0.10 poststocking (Avila et al. 2018) and ranged from 0.02 to 0.29 among the streams. Growth differed among strain and streams only in the short-term (2-month) period (Avila et al. 2018). To determine which habitat variables accounted for differences in 2-month apparent survival and growth, both between the Rainbow Trout strains and among the nine streams in which these fish were stocked, linear models were constructed and evaluated using the information theoretic approach (Burnham and Anderson 2002). To evaluate the effects of individual habitat variables, each factor was considered separately in an individual model and in an additive effect model (strain in addition to the different habitat variables) and included intercept models for both strain and stream. The combination of factors affecting survival (average temperature, entrenchment ratio, D_{50} , predator numbers, and competitor biomass) resulted in a total of 32 models in the survival model set (n = 9; streams) and the combination of factors affecting growth (strain, average

temperature, predator number, and competitor biomass) resulted in 16 models in the growth model set (n = 18; nine streams × two strains). Akaike's information criterion using second-order approximations (AIC_c) was used to rank the models. We selected models based on Akaike AIC_c differences (Δ AIC_c < 4), and we report model weights (w_i) and parameter estimates with their associated 95% confidence intervals (CIs) from the top supported model in which and individual factor appeared (Burnham and Anderson 2002).

RESULTS

Apparent Survival by Stream

The AIC_c analysis indicated that short-term apparent survival was most affected by differences in average temperature among the streams (Δ AIC_c=0, w_1 =0.41; Table 1) with the only other model with comparable performance being the intercept only model (Δ AIC_c=0.43, w_2 =0.33; Table 1). In general, streams with warmer average temperature were associated with higher short-term apparent survival (Figure 1), although the 95% confidence intervals included zero (β_{temp} =0.060 [CI = -0.0004, 0.120]). Our results also indicate that average pebble size (D_{50}) and entrenchment ratio may reduce apparent survival (Table 1), but the effects were small and the associated 95% confidence intervals included zero (β_{D50} = -0.003 [CI = -0.009, 0.003]; $\beta_{\text{entrenchment}}$ = -0.006 [CI = -0.021, 0.008]).

Growth

We used stream characteristics to describe potential mechanisms that could explain growth differences. The top model contained strain, average temperature, competitor biomass, and predator numbers as factors that affected growth ($\Delta AIC_c = 0$, $w_1 = 0.44$; Table 2). Strain appeared in all supported models with a ΔAIC_c less than 4 (cumulative AIC_c weight = 0.88; Table 2). The $GR \times CRR$ strain exhibited a higher growth rate than the GR, with a difference in growth rate between the two strains of 4.52 mm/month (SD = 1.72), and growth rates were affected by average stream temperature (cumulative AIC_c weight = 0.75; Table 2). Streams with warmer average temperatures were associated with higher growth rates ($\beta_{temp} = 1.55$ [CI = 0.56, 2.53]; Figure 2). Similarly, although the effects were small, higher predator numbers were associated with higher growth rates ($\beta_{predator\ number} = 0.01$ [CI = 0.002, 0.03]), but lower growth rates were associated with higher competitor biomass ($\beta_{competitor\ biomass} = -0.002$ [CI = -0.003, -0.0002]; Table 2; Figure 3).

DISCUSSION

The main objective of our study was to conduct a supplementary analysis to Avila et al. (2018) and estimate shortterm apparent survival and growth of two resistant strains of Rainbow Trout. We deliberately chose streams that were qualitatively similar to minimize the effect of stream characteristics on our estimates because our study was not designed to assess effects of habitat per se. However, our previous results indicated that stocking location (stream) influenced both short-term apparent survival and growth (Avila et al. 2018). We anticipated that both biotic and abiotic stream characteristics (e.g., average temperature, number of predators, competitor biomass, and average substrate size) resulted in variation in our apparent survival and growth estimates. However, we did not consider bottom-up food web processes (e.g., primary productivity) and anthropogenic factors such as angling (leading to disruption of habitat and

TABLE 1. Model selection results (models with a model weight>0) examining the effects of stream covariates on short-term (2-month) poststocking apparent survival of Rainbow Trout stocked in nine Colorado streams. Included are R^2 values, the log likelihood (logLik), number of parameters (K), Akaike's information criterion corrected for small sample size (AIC_c), the difference in AIC_c values (Δ AIC_c), and AIC_c model weight (w_i). The models with a Δ AIC_c value less than 4 were considered as contributing information to covariates affecting Rainbow Trout survival.

Model	R^2	K	logLik	AIC_c	$\Delta { m AIC}_c$	Weight (w _i)
Average temperature	0.44	2	11.7	-12.6	0	0.41
Intercept	0	1	9.1	-12.2	0.43	0.33
D_{50}	0.16	2	9.9	-8.9	3.7	0.063
Entrenchment	0.13	2	9.7	-8.7	4.0	0.055
Competitor biomass	0.037	2	9.3	-7.8	4.9	0.035
Predator number	0.001	2	9.1	-7.4	5.2	0.029
Average temperature + competitor biomass	0.54	3	12.6	-7.2	5.5	0.026
Average temperature $+D_{50}$	0.52	3	12.4	-6.8	5.9	0.022
Average temperature + entrenchment	0.44	3	11.7	-5.5	7.2	0.011
Average temperature + predator number	0.44	3	11.7	-5.5	7.2	0.011
D_{50} + entrenchment	0.27	3	10.5	-3.02	9.6	0.0033
D_{50} + predator number	0.22	3	10.2	-2.5	10.2	0.0025
Competitor biomass + D_{50}	0.18	3	9.9	-1.9	10.7	0.002

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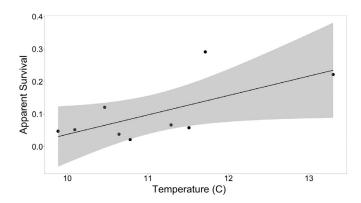


FIGURE 1. Relation between average stream temperature (°C) and average apparent survival of Rainbow Trout 2-months poststocking as fry. The dots represent the average survival and average temperature for each of the nine streams. The gray shaded area represents the 95% confidence interval for the trend line describing the data points. Apparent survival did not differ between the two Rainbow Trout strains, so the data were pooled.

removal of predators), area use (vehicles), or the presence of terrestrial predators. Our results indicate that some stream characteristics are important short-term determinants of Rainbow Trout performance after stocking and may account for the differences that we observed among stocking locations.

Temperature was the top abiotic variable that positively influenced overall Rainbow Trout survival within the average temperature range across the nine streams (9.9–13.3°C). River temperature during the fry stage of

Chum Salmon Oncorhynchus keta has been linked to variation in survivorship despite the majority of life spent at sea (Morita et al. 2015), indicating that abiotic variables such as temperature are important factors to consider when introducing fish into the wild. The effect of temperature that we estimated was observed in 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 (Elliott 1975; Austreng et al. 1987). Although the 95% confidence intervals of the effect of average temperature on short-term apparent survival slightly overlapped with zero, as well as the second top model (intercept-only model) having almost as much support, which could indicate no overall effect on apparent survival, the vast majority of the effect was positive and effect size was larger than the other predictor variables. The estimated effect size and the span of the 95% confidence intervals of the effect of temperature between August and September indicates that stocking age-0 trout during the pre-fall season and into streams that have temperatures around 12-13°C and are not very cold may be beneficial for growth and survival.

An advantage that the GR × CRR strain showed over the pure GR strain was a higher growth rate. Growth rate may be an important factor for higher survival and reestablishing fish populations in natural environments. Most fish show age-specific mortality, where younger, smallerbodied fish have higher mortality due to predation (Sogard 1997). The ability to overcome predation in

TABLE 2. Model selection results (models with a model weight>0) examining the effects of stream covariates thought to affect the short-term (2 month) poststocking growth rate (mm/month) of Rainbow Trout stocked in nine Colorado streams. Included are R^2 values, the number of parameters (K), log likelihood (logLik), Akaike's information criterion corrected for small sample size (AIC $_c$), the difference in AIC $_c$ values (Δ AIC $_c$), and AIC $_c$ model weight (w_i). The models with a Δ AIC $_c$ value less than 4 were considered as contributing information to covariates affecting Rainbow Trout growth rate.

Model	R^2	K	logLik	AIC_c	$\Delta { m AIC}_c$	Weight (w _i)
Strain + average temperature + competitor biomass + predator number	0.78	6	-33.8	87.32	0	0.44
Strain + average temperature	0.61	3	-39.0	89.08	1.8	0.18
Strain + average temperature + predator number	0.67	4	-37.4	89.71	2.4	0.13
Strain + average temperature + competitor biomass	0.67	4	-37.4	89.76	2.4	0.13
Strain	0.45	2	-42.1	91.82	4.5	0.05
Strain + predator number	0.52	3	-40.8	92.71	5.4	0.03
Strain + competitor biomass	0.48	3	-41.5	94.08	6.8	0.015
Strain + competitor biomass + predator number	0.58	4	-39.5	94.08	6.8	0.015
Average temperature	0.16	2	-45.9	99.44	12.1	0.001
Intercept	0	1	-47.4	99.63	12.3	0.001
Predator number	0.071	2	-46.8	101.2	13.9	0.0004
Average temperature + predator number	0.22	3	-45.1	101.3	14.01	0.0004
Average temperature + competitor biomass	0.22	3	-45.1	101.4	14.04	0.0004
Competitor biomass	0.032	2	-47.1	101.9	14.6	0.0003
Average temperature + competitor biomass + predator number	0.33	4	-43.8	102.6	15.3	0.0002
Competitor biomass + predator number	0.13	2	-46.1	103.3	16.0	0.0001

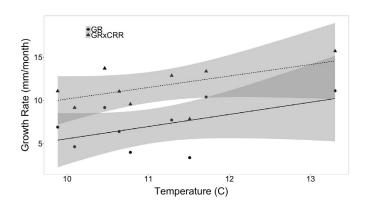


FIGURE 2. Predicted growth rates compared with average stream temperature (°C) for GR (circles; solid line) and $GR \times CRR$ (triangles; dotted line) 2 months poststocking as fry. The gray shaded areas represent the 95% confidence intervals for the trend lines describing the data points.

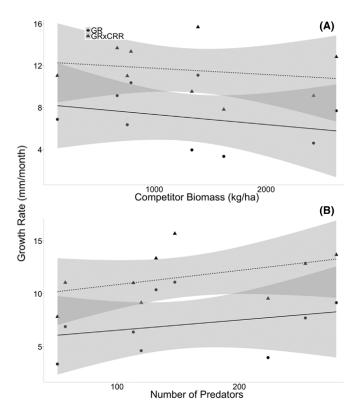


FIGURE 3. Predicted growth rates compared with (A) competitor biomass and (B) predator numbers for GR (circles; solid line) and GR \times CRR (triangles; dotted line) 2 months poststocking as fry. The gray shaded areas represent the 95% confidence intervals for the trend lines describing the data points.

younger age-classes may be the result of juveniles growing fast enough to overcome the gape limit of the predators (Nilsson and Bronmark 2000; Scharf et al. 2000) or that fry may more easily recognize the threat of predation after their first encounter with predators (Kopack et al. 2015).

Traditionally, growth rate declines with increased competition or density within the environment (Jenkins et al. 1999; Vøllestad et al. 2002). Despite a downward trend of growth rate when competitor biomass increases, the GR × CRR strain showed higher growth rate compared with the pure GR strain, which was opposite of what has been observed within the laboratory (GR have higher growth compared with GR × CRR; Fetherman et al. 2011). The GR × CRR strain may have exhibited more wild characteristics due to the CRR genes and demonstrated higher dominance behaviors by maintaining profitable stream habitat locations to increase or maintain foraging (Fausch 1984), leading to the benefit of higher growth rates compared with the pure GR strain.

Our supplementary analysis of the habitat data indicates that the GR strain may be at a disadvantage due to slower growth rates across the temperature range as well as competitor and predator biomass. Slower growth indicates that using the GR strain to avoid the loss of whirling disease resistance caused by outcrossing and backcrossing (Schisler et al. 2006; Fetherman et al. 2011, 2012) may need further consideration depending on site-level habitat characteristics. Choosing the correct stocking locations may be important to maximize survival and growth of the GR so that it may be used as a M. cerebralis-resistant management option. Development of whirling-disease-resistant Rainbow Trout for management of M. cerebralis within Colorado has been ongoing for the past 2 decades (Schisler et al. 2006; Fetherman et al. 2011, 2012, 2014; Avila et al. 2018, 2022); however, further poststocking studies into long-term survival, growth, reproduction, and movement of the GR strain in the wild would be beneficial. Additionally, the prevalence and severity of whirling disease as well as the potential negative effects of other pathogens (e.g., Avila et al. 2022) would ideally be investigated for each Rainbow Trout strain.

There are experimental and analytical limitations to this study. In our current analysis, average temperature was the top model describing apparent survival differences, despite temperatures that only ranged 3.4°C among streams. However, there is model selection uncertainty, as the second model showed support for no temperature effect or rather no factors affecting short-term apparent survival (intercept-only model). The lack of a clear temperature effect could be a result of how streams were selected or how many streams were included in the study. Only nine streams across Colorado were used, and all streams were selected to be both qualitatively similar and relatively small. To further investigate the biotic and abiotic factors that affect Rainbow Trout poststocking survival and growth, as well as to potentially reduce model selection uncertainty, our study would have benefited from selecting a higher number of streams with more variable habitat characteristics or stream sizes. Additionally, incorporating other factors such as, bottom-up food web

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processes (e.g., habitat elements acting indirectly on primary productivity and therefore growth), anthropogenic factors such as angling (leading to disruption of habitat and removal of predators), area use (e.g., vehicles disrupting the area or cattle grazing changing the riparian zone), or the presence of terrestrial predators could help explain differences in survival and growth in future studies.

Our study indicates that biotic and abiotic factors affect short-term whirling disease resistant Rainbow Trout poststocking survival and growth rate. When managing stream populations for reintroduction of disease resistant strains of fish, consideration of potential biotic and abiotic factors that may affect survival and growth, even in streams that are considered similar to one another, would be useful.

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