

ORIGINAL ARTICLE

Intrinsic and extrinsic drivers of life-history variability for a south-western cutthroat trout

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Abstract

The impacts of climate change on cold-water fishes will likely negatively manifest in populations at the trailing edge of their distributions. Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*, RGCT) occupy arid south-western U.S. streams at the southern-most edge of all cutthroat trout distributions, making RGCT particularly vulnerable to the anticipated warming and drying in this region. We hypothesised that RGCT possess a portfolio of life-history traits that aid in their persistence within streams of varying temperature and stream drying conditions. We used otolith and multistate capture–mark–recapture data to determine how these environmental constraints influence life-history trait expression (length- and age-at-maturity) and demography in RGCT populations from northern New Mexico, United States. We found evidence that RGCT reached maturity fastest at sites with warm stream temperatures and low densities. We did not find a strong relationship between discharge and any demographic rate, although apparent survival of mature RGCT decreased as stream temperature increased. Our study suggests plasticity in trait expression may be a life-history characteristic which can assist trailing edge populations like RGCT persist in a changing climate.

KEYWORDS

density-dependent, density-independent, lester model, multistate capture–mark–recapture, peripheral populations, Rio Grande cutthroat trout

1 | INTRODUCTION

A major goal in conservation is to preserve diversity across scales of biological organisation, from genetics to meta-communities. High genetic diversity promotes species resiliency through adaptive capacity (Healey, 2009), while ecological resiliency benefits from the direct relationship between species and functional diversity (Peterson, Allen, & Holling, 1998). Life-history trait expression represents an important source of diversity that can affect persistence of populations (Jager, 2001; Lande, 1988; Schindler et al., 2010) by stabilising populations subject to stochastic environmental

conditions (Healey, 2009; Hutchings & Myers, 1994; Moore, Yeakel, Peard, Lough, & Beere, 2014). For example, asynchronous population dynamics among subpopulations in response to heterogeneous environmental conditions can improve resilience of an entire meta-population (Reed, Schindler, & Waples, 2011; Schindler et al., 2010). The extent to which habitat alterations and a changing climate may eliminate available habitats (e.g. loss of river main stems for mobile fish life-history forms, Williams, Haak, Neville, & Colyer, 2009) may exacerbate the extirpation risk for many species. This includes the loss of stabilising properties that accompany diverse life-history trait expression common in healthy populations

(Anderson, Ousterhout, Peterman, Drake, & Semlitsch, 2015; Moore et al., 2014; Reed et al., 2011).

Life history is defined by Ricklefs and Wikelski (2002) as behavioural, physiological and anatomical adaptations that directly affect survival and reproduction, which are measures of demographic success. Fluctuations in temperature, precipitation, available food and other stochastic environmental conditions (e.g. wildfire) are particularly important for fishes as these conditions are affiliated with demographic performance and ultimately the evolution of life-history traits (Olden & Kennard, 2010; Reznick, Bryga, & Endler, 1990; Winemiller, 2005; Winemiller & Rose, 1992). For example, body size directly correlates with reproductive potential for many aquatic ectotherms, but significant physiological costs occur as temperatures increase for larger- compared to smaller-bodied individuals (Daufresne, Lengfellner, & Sommer, 2009; Sheridan & Bickford, 2011). Thus, faster life-history traits (e.g. early maturation, high fecundity) are favoured in environments where adult mortality is high, while slower life-history traits (e.g. delayed maturation, low fecundity) are favoured when environmental fluctuations more strongly affect early life stages (Cayuela et al., 2016). Both extrinsic (density-independent) and intrinsic (density-dependent) mechanisms are important in affecting stage-specific mortality risk and reproductive success in fishes, playing a critical role in shaping life-history traits among different species (Olden & Kennard, 2010; Winemiller, 2005) and among different populations of the same species (Ward, Post, Lester, Askey, & Godin, 2017).

Cutthroat trout (*Oncorhynchus clarkii*) have a broad spatial distribution (western North America) and diverse life-history traits that aid in persistence within the many dynamic environments they inhabit (Penaluna et al., 2016). Whether anadromy or potamodromy, migratory movements are commonly presented as examples of the various life-history traits expressed by cutthroat trout (Gresswell, Liss, & Larson, 1994; Homel, Gresswell, & Kershner, 2015). However, many populations of cutthroat trout persist above natural and man-made barriers, environments that preclude a migratory life-history trait (Harig & Fausch, 2002; Peterson, Rieman, Dunham, Fausch, & Young, 2008; Zeigler, Rogers, Roberts, Todd, & Fausch, 2019). Interestingly, these trout populations persist by adapting to the demographic pressures within isolation, favouring life-history traits that often reflect a faster pace of life (e.g. earlier maturity, faster somatic growth; Morita, Yamamoto, & Hoshino, 2000; Morita, Morita, & Yamamoto, 2009; Letcher, Nislow, Coombs, O'Donnell, & Dubreuil, 2007; Carim, Vindenes, Eby, Barfoot, & Vøllestad, 2017). Thus, one can elucidate the potential for local cutthroat trout populations to persist as environmental conditions continue to change by determining if environmental pressures favour certain life-history traits on the landscape via demography.

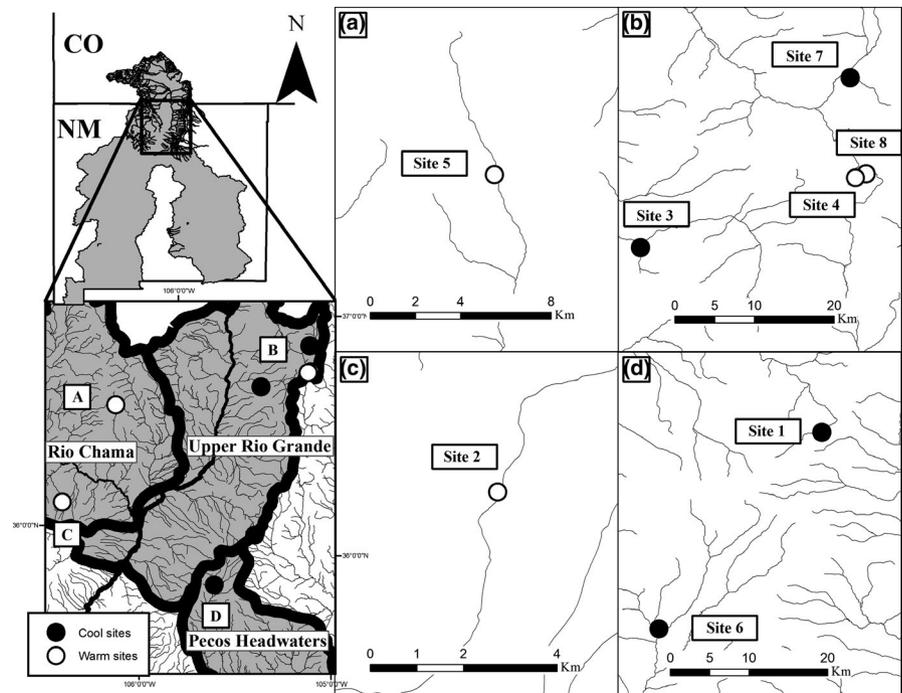
Rio Grande cutthroat trout (*O. c. virginalis*, RGCT) is native to the Rio Grande, Canadian and Pecos Rivers in New Mexico and Colorado (Figure 1) at the southern periphery of all cutthroat trout distributions and thus harbingers of large-scale ecological disturbances such as climate change (Bakevich, Paggen, & Felt, 2019; Behnke, 2002; Hampe & Petit, 2005). Haak, Williams, Neville, Dauwalter, and

Colyer (2010) demonstrated edge populations of cutthroat trout have experienced the greatest loss in occupied habitat and RGCT is no exception, where they currently occupy less than 12% of their historical range due to invasive species, climate change, disease and habitat loss (Bakevich et al., 2019; Zeigler et al., 2019). Nearly all contemporary populations occur within isolated high-elevation stream segments (Bakevich et al., 2019), a potential fate for many trout species (particularly cutthroat trout) in the conterminous United States in response to warming temperatures and altered stream flows due to a changing climate (Isaak et al., 2016; Isaak, Young, Nagel, Horan, & Groce, 2015; Roberts, Fausch, Peterson, & Hooten, 2013; Wenger et al., 2011). Effective management of isolated RGCT populations in the future will surely benefit from evaluating how environmental characteristics affect RGCT persistence through demography.

Most evidence suggests that RGCT population dynamics are shaped by extrinsic environmental conditions (Bakevich et al., 2019; Huntsman, Martin, & Patten, 2018). For example, air temperature has increased and precipitation has decreased throughout the intermountain West in recent decades (Isaak et al., 2012; Zeigler, Todd, & Caldwell, 2012), resulting in streams once supporting healthy RGCT populations going intermittent (Zeigler et al., 2012). These streams also commonly exceeded thermal limits during much of the summer (upper incipient limit of 21.7°C; Zeigler et al., 2013; Zeigler et al., 2012) which, along with drought, are among the most common environmental constraints directly linked to demographic performance of cutthroat trout populations (Kovach et al., 2016). However, many RGCT populations are isolated within high-elevation streams that are likely buffered against a warming climate (sensu Isaak et al., 2016; Isaak et al., 2015), and a recent study indicates temperature and flow have a relatively minor impact on RGCT persistence relative to other pressing concerns (namely, non-native species; Zeigler et al., 2019). Furthermore, cutthroat trout recruitment is limited by cool temperatures in high-elevation streams (Coleman & Fausch, 2007), which may partially explain the quadratic relationship between RGCT abundance and temperature found by Huntsman et al. (2018). Regulation around an internal carrying capacity set by competition for limiting resources (e.g. competition for food) may play an important role shaping life-history traits of many isolated RGCT populations, as has been detected in many salmonid studies (Grossman & Simon, 2019). Consequently, RGCT populations occur in streams across a range of intrinsic (density) and extrinsic (e.g. temperature, intermittency) environmental conditions (Bakevich et al., 2019) that could potentially influence life-history trait expression.

Here, we evaluated how intrinsic and extrinsic factors interact to affect RGCT life-history traits to better understand the extent to which RGCT may be resilient to uncertain future conditions. We hypothesised that RGCT life-history strategies would vary from "slow" to "fast" due to the risk of RGCT mortality from extrinsic environmental conditions. "Slow" life-history traits were expected in streams characterised as high-density, cool and perennial. "Fast" life-history traits were expected in low-density, warm and intermittent streams because RGCT is a stenothermic cold-water species

FIGURE 1 Sampling streams for Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) in northern New Mexico. Warm streams were defined by the occurrence of maximum daily stream temperatures exceeding 21.7°C, and cool streams were defined by maximum daily stream temperatures never exceeding 21.7°C



and thus less likely to reach older age-classes in warm-intermittent streams. We tested this hypothesis by identifying lengths and ages at which RGCT reach maturity in streams across these density, temperature and intermittency gradients. We then employed multistate capture-mark-recapture methods to determine how density-independent (e.g. temperature, flow) and density-dependent mechanisms affected maturation transition probabilities and survival rates of immature and mature RGCT.

2 | METHODS

2.1 | Study sites

We selected eight study sites within northern New Mexico that covered a range of temperature and intermittency conditions as a space-for-time sampling design to improve our chances of capturing the range of environmental conditions RGCT would experience over an extended period of time, without the benefit of a long-term data set. The majority of streamflow in this arid region is supplied by snowmelt, where snow contributes as much as 75% of annual flow in the upper Rio Grande basin (Rango, 2006). Our sites were chosen based on three criteria: risk of the maximum weekly average stream temperature (MWAT) exceeding the 30-day ultimate upper incipient lethal temperature for juvenile RGCT (21.7°C; Zeigler et al., 2013), history of stream intermittency, and relatively high RGCT densities to ensure sufficient recaptures would be available to estimate demographic rates using capture-mark-recapture methods. However, our sampling occurred during two of the wettest years of the decade (Figure S1) that likely impacted our ability to detect drought-like conditions on population dynamics within our study sites. Four of

our eight sites exhibited maximum daily temperatures that exceeded 21.7°C during at least one day during our study and confirmed their classification as warm RGCT sites (Table 1, Figure 1). Site selection was further constrained by a factorial design based on intermittency and temperature treatments (Zeigler et al., 2012), where four sites were previously found to dry in at least a small section of the stream (cool-intermittent = sites 6 and 7, warm-intermittent = sites 2 and 4) and the remaining four sites were perennial (cool-perennial = sites 1 and 3, warm-perennial = sites 5 and 8; Figure 1). All sample sites were established above fish barriers because low RGCT abundances typically occur when non-native trout are present and we wanted to control for a non-native trout effect (Bakevich et al., 2019). Therefore, non-native trout were not anticipated; however, brown trout (*Salmo trutta*) were more abundant above the barrier (mean density = 0.083 ± 0.016 s.e. #/m stream length) than RGCT (mean density = 0.022 ± 0.005 s.e. #/m stream length) at the cool-perennial site 3.

We sampled the same stream segments within all eight sites in the spring (May–June), summer (July–August) and fall (September–October) of 2016 and 2017 (Figure 1, Table 1 and Table S1). Rio Grande cutthroat trout were captured during each sampling occasion by backpack electrofishing (Smith-Root LR-24) within a 300-m study site. We chose 300 m because this length of stream could be sampled by three-pass depletion within one sampling day and would provide the greatest chance of recapturing tagged fish. However, equipment failure resulted in a single pass or only two passes on four occasions. We further delineated each 300-m site into six continuous 50-m segments so that RGCT could be processed and released near their point of capture. All fish were measured for length (total length, ± 1 mm) and weight (± 0.1 g), and RGCT greater than 60 mm total length (TL) were implanted with

TABLE 1 Habitat and Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) capture and recapture information for each sampling stream in northern New Mexico. Number of days maximum daily temperatures exceeded 21.7°C in 2016 and 2017 is represented by No. days above 21.7°C. Mean daily temperature between spring and summer sampling is in degrees Celsius; summer discharge is the measured discharge (cubic metres per second, m³/s) during summer sampling. Mean density is the mean number of RGCT (tagged and not tagged) captured on the first depletion sampling pass during each sampling occasion divided by stream length sampled (#/m stream length). The total number of fish tagged and number of tagged fish recaptured at least once during the study are reported in the “No. tagged” and “No. recaptured” columns, respectively. The * indicates that missing temperature loggers prevented a full summation of the number of days above the 21.7°C. Mean spring–summer temperatures for that site were estimated from a temperature regression equation with site 8. Values in parentheses are standard errors. “Site type” indicates whether a stream is a warm, cool, perennial (Per.) or intermittent (Int.) stream. Sites 1–8 are commonly referred to as Alamitos, Cañones, Columbine, Comanche, El Rito, Jacks, Powderhouse and Vidal, respectively. Sites 1, 2 and 3 are streams referenced in Huntsman et al. (2018)

Site	Site type	Barrier	No. days above 21.7°C		Mean spring–summer temperature		Summer discharge (m ³ /s)		Depth (cm)		Mean density	No. tagged	No. recap
			2016	2017	2016	2017	2016	2017	2016	2017			
Site 1	Cool-Per.	Man-made	0	7.8	9.2	0.145	0.182	24.9 (7.1)	18.3 (6.5)	0.313 (0.050)	394	189	
Site 2	Warm-Int.	Man-made	46	13.2	14.9	0.007	0.031	12.9 (7.6)	14.0 (7.5)	0.174 (0.016)	201	98	
Site 3	Cool-Per.	Natural	0	7.5	8.4	0.272	0.331	32.2 (10.9)	27.4 (7.9)	0.022 (0.005)	34	18	
Site 4*	Warm-Int.	Man-made	37	14.3	15.0	0.006	0.220	20.9 (12.8)	20.0 (11.1)	0.031 (0.009)	43	15	
Site 5	Warm-Per.	Man-made	5	14.0	13.3	0.102	0.119	17.0 (7.4)	16.3 (5.3)	0.155 (0.051)	148	67	
Site 6	Cool-Int.	Man-made	0	11.3	10.1	0.028	1.601	20.4 (7.9)	17.0 (8.1)	0.388 (0.029)	441	241	
Site 7	Cool-Int.	Man-made	0	10.0	10.9	0.001	0.025	9.9 (5.0)	10.7 (5.6)	0.238 (0.040)	247	101	
Site 8	Warm-Per.	Man-made	36	13.7	14.4	0.000	0.016	16.6 (11.7)	14.4 (8.9)	0.033 (0.009)	44	20	

either an 8 mm (fish smaller than 80 mm) or 12 mm (fish 80 mm or larger) full-duplex (FDX) passive integrated transponder (PIT; Oregon RFID, Portland, Oregon) tag if they did not already possess a tag. Lastly, stream discharge (m³/s) was estimated at the same single downstream location on each sampling occasion using the area-velocity approach (HACH digital flow meter; Gore & Banning, 2017).

2.2 | Stream temperature and habitat

To monitor stream temperature and intermittency, two ProV2® (Onset Computer Corporation, Bourne, MA, USA) temperature loggers as well as two intermittency loggers were deployed in two separate pools and riffles within each site. The intermittency loggers are a modified Hobo Pendant® data logger (Onset Computer Corporation) that enables simultaneous collection of high-resolution water temperature and electrical resistance (Chapin, Todd, & Zeigler, 2014). This single, multi-functional sensor can reliably collect temperature and can infer wet versus dry stream conditions. Logger failure and displaced data loggers resulted in stream temperature not being recorded at site 4 from 10 June 2017 to 31 October 2017 or at site 8 from 1 October 2016 to 9 June 2017 (Figure S2). We fit a linear regression between site 8 and site 4 mean daily temperatures when both were available (site 4 temperature = $-0.05 + 1.05 \times \text{site 8 temperature}$, $R^2 = 0.84$, $p < .001$) and used the resulting linear equation to fill in missing temperature data for each site (Figure S3).

During low flows (early July 2016 and late August–early September 2017), stream depth and large-woody debris volume were measured within each site. Every three metres for the entire 300-m study site, a depth measurement was taken within the thalweg as an indicator of the minimum amount of potential drought refugia available within each site for each summer. We used large-woody debris volume within each site from habitat surveys to account for potential bias in our ability to capture and recapture RGCT during surveys (see below). All large-woody debris (LWD) was recorded within each site, and a relative LWD volume was calculated using similar methods as Huntsman and Falke (2019). All LWD was counted and assigned to a length bin at approximately 1.5-m intervals (1.5–3.0, 3.0–4.5, 4.5–6 and >6 m) and a width bin at approximately 10-cm intervals (10–20, 20–30, 30–40, 40–50 and >50 cm). We estimated LWD volume by ranking each bin length and width, and then multiplying both bin ranks by the quantity of LWD in those categories. For example, three pieces of LWD within the largest length (rank = 4) and width (rank = 5) bins would have an LWD volume of 60 (e.g. 3 pieces $\times 4 \times 5 = 60$).

2.3 | Multistate Capture–Mark–Recapture (CMR) analysis

We defined two RGCT states for our multistate demographic model, immature and mature RGCT. We identified immature (I) and

mature (M) RGCT states based on a length-at-maturity threshold, identified within cool and warm sites by a Lester growth model (Lester, Shuter, & Abrams, 2004; Ward et al., 2017; Wilson, Honsey, Moe, & Venturelli, 2018). The Lester growth model is a biphasic derivation of the von Bertalanffy growth curve where two separate lines are fit to length-at-age data. One curve is assumed linear because it is fit to the growth of immature fish that do not partition energy into reproduction. The second curve is fit to mature growth, which is the typical von Bertalanffy curve where energy is partitioned away from somatic growth into gamete production (Honsey, Staples, & Venturelli, 2017; Wilson et al., 2018). We fit the Lester model to RGCT otolith data published in Huntsman et al. (2018), where otoliths were extracted from 247 RGCT in 2010 from one warm site (site 2; $n = 98$) and two cool sites (site 1; $n = 88$ and site 3; $n = 61$). Aged otoliths and RGCT lengths were then incorporated into a biphasic growth model with the following form (Wilson et al., 2018):

$$l_t = \begin{cases} h(t - t_1), & t \leq T \\ L_\infty (1 - e^{-k(t - t_0)}), & \text{otherwise} \end{cases} \quad (1)$$

where l_t is length at time t (year), h is immature growth rate (mm length per year), t_1 is the Lester model hypothetical age-at-length 0, T is age-at-maturity, L_∞ is the asymptotic size parameter, k is the rate at which L_∞ is reached and t_0 is the von Bertalanffy hypothetical age-at-length 0. Trade-offs among reproduction, mortality and growth can be shown to be reflected in L_∞ , k and t_0 with the following equations (Lester et al., 2004; Wilson et al., 2018):

$$L_\infty = \frac{3h}{g} \quad (2)$$

$$k = \ln \left(1 + \frac{g}{3} \right) \quad (3)$$

$$t_0 = T + \frac{\ln \left(1 - \frac{g(T - t_1)}{3} \right)}{\ln \left(1 + \frac{g}{3} \right)} \quad (4)$$

where g is an energetic cost of maturity to somatic growth. We adopted a Bayesian framework to implement the biphasic growth model. We specified vague priors with a large variance (*i.e.* small precision) for all parameters in the biphasic growth model where $h \sim \text{Normal}(0, 1,000) \text{Tr}(0)$, (*i.e.* a truncated normal distribution with a

lower bound of zero), $T \sim \text{Uniform}(0, \text{max age})$, $t_1 \sim \text{Normal}(0, 10)$ and $g \sim \text{Normal}(0, 100) \text{Tr}(0, 3/(T - t_1))$. The *max age* observed from otolith data was 9 years. The energetic cost of maturity was truncated (Tr) at the lower end by 0 and upper end by $3/(T - t_1)$, a necessary energetic constraint described in Wilson et al. (2018) because an individual cannot allocate more energy into reproduction than would be available for growth if that individual was to continue growth as an immature fish. We then ran two separate growth models with and without a temperature effect (a warm or cool categorical variable) on the g , h and T parameters. We used deviance information criterion (DIC), an information theoretic approach to model selection used in Bayesian analyses (Spiegelhalter, Best, Carlin, & van der Linde, 2014), to determine the importance of temperature on RGCT maturation size and age. We considered a $\Delta \text{DIC} > 7$ (DIC model 1 - DIC model 2) as sufficient evidence for differences between models in model fit (Cain & Zhang, 2019; Spiegelhalter, Best, Carlin, & van der Linde, 2002). We estimated length-at-maturity from the model with the lowest DIC by substituting T in for t in Equation 1, which the immature size-class was defined as RGCT with total length less than the estimated length-at-maturity. The mature size-class was defined as any fish at or exceeding the size necessary to reach maturity (Figure 2). We used Markov chain Monte Carlo (MCMC) algorithms and conducted full Bayesian inference using the program JAGS (version 3.4; Plummer, Stukalov, Denwood, & Plummer, 2016) executed from R (R Core Team, 2019) with the package jagsUI (Kellner, 2015). Posterior distributions were generated from three independent chains with length of 110,000 iterations, a thinning of 50, three chains and a burn-in of 10,000. Model convergence was assessed by examining Gelman-Rubin convergence diagnostics ($R < 1.1$; Gelman & Rubin, 1992).

We used a multistate CMR model for open populations (Lebreton, Nichols, Barker, Pradel, & Spendelov, 2009; Nichols & Kendall, 1995) with a Bayesian state-space approach (Calvert et al., 2009; Kéry & Schaub, 2011) to estimate the apparent survival (ϕ), transition (Ψ) and recapture (p) probabilities of RGCT based on immature and mature states defined by the Lester analysis. We defined three true states and three observed states. The true states were alive as immature, alive as a mature trout and dead, whereas the observed states were seen as immature, seen as a mature trout and not seen. The simplified version of our multistate model can be expressed in the form of survival-transition state and observation matrices (Table 2). We used the following logit-linear regression equations to assess the effects of covariates, which were standardised by subtracting the mean and dividing by the standard deviation, on demographic and detection parameters.

For survival probabilities:

$$\begin{aligned} \text{logit}(\phi_{\text{immature or mature}}) &= \alpha + w_1 * \beta_1 * \text{Temp}_{iz} + w_2 * \beta_2 * \text{Density}_{it-1} + w_3 * \beta_3 * Q_{iz} \\ &+ w_4 * \beta_4 * \text{Depth}_{iy} + \beta_5 * \text{Interval}_z + \varepsilon_{\phi_i} \\ \varepsilon_{\phi_i} &\sim \text{Normal}(0, \sigma_\phi^2) \end{aligned} \quad (5)$$

For transition probabilities:

$$\begin{aligned} \text{logit}(\Psi_{\text{immature-mature}}) &= \alpha + w_1 * \beta_1 * \text{DegreeDay}_{iz} + w_2 * \beta_2 * \text{DegreeDay}_{iz}^2 + w_3 * \beta_3 * Q_{iz} \\ &+ w_4 * \beta_4 * \text{Density}_{it-2} + w_5 * \beta_5 * \text{DegreeDay}_{iz} * \text{Density}_{it-1} \\ &+ w_6 * \beta_6 * \text{DegreeDay}_{iz}^2 * \text{Density}_{it-1} + \beta_7 * \text{Interval}_z + \varepsilon_{\Psi_i} \\ \varepsilon_{\Psi_i} &\sim \text{Normal}(0, \sigma_{\Psi}^2) \end{aligned} \tag{6}$$

For detection probability:

$$\begin{aligned} \text{logit}(p_{\text{immature or mature}}) &= \alpha + w_1 * \beta_1 * \text{LWD}_{iy} + w_2 * \beta_2 * Q_{it} + \varepsilon_{pi} \\ \varepsilon_{pi} &\sim \text{Normal}(0, \sigma_p^2) \end{aligned} \tag{7}$$

where w is an indicator variable used for model selection (Kuo & Mallick, 1998, *see below*), and $Temp$ and $Degree Day$ are the average mean daily temperature and cumulative number of degree days between sampling intervals z (e.g. spring-summer 2017) for site i , respectively. Both large-woody debris (LWD) and mean depth ($Depth$) were collected in the summer of each year y , Q is stream discharge collected on each sampling occasion (t) with the mean between sampling intervals (z) used as a predictor variable affecting vital rates, $interval$ is the number of months between sampling occasions, and ε s are a random effect at the site level (i) for each demographic parameter. We used the mean temperature and stream discharge between sampling occasions to model vital rates, similar to approaches taken for modelling seasonal vital rates of other trout populations (Letcher et al., 2015). Degree days were used instead of mean daily temperature to constrain our transition rate (Ψ) because this demographic rate is a proxy for instantaneous growth and development and degree days are commonly used to model temperature effects on growth in fishes (Huntsman

et al., 2018; Ward et al., 2017). Degree days were calculated based on the following equation:

$$\text{Degree Days} = \sum_{x=1}^n \text{Temp}_{ix} - T_0 \tag{8}$$

where $Temp$ is mean daily temperature for day x of n total days and T_0 is the minimum temperature at which growth typically occurs in cutthroat trout (5°C, Coleman & Fausch, 2007; USFWS, 1998). $Density$ is effective density on each sampling occasion t and for site i defined as follows:

$$\text{Density}_{it} = \frac{\sum_{d=1}^n (\text{Trout Length}_{id})^2}{\text{Stream Area}_{it}} \tag{9}$$

where d is an index for each individual trout (both RGCT and brown trout at site 3) of all n trout (Post, Parkinson, & Johnston, 1999; Ward et al., 2017). We used density during sampling event $t-1$ to assess whether there was evidence of negative density dependence on vital rates (Grossman, Ratajczak, Wagner, & Petty, 2010). We included a quadratic temperature effect on our transition parameter because summer temperatures at our warmer sites often exceeded the optimal

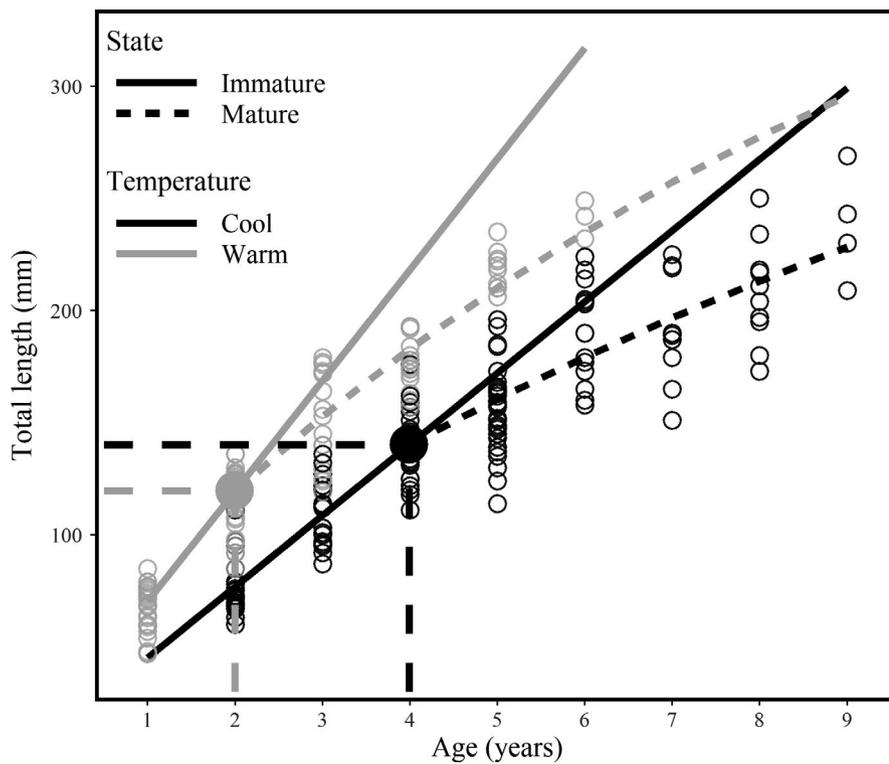


FIGURE 2 Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) length-at-age fitted with a Lester growth model to identify length and age-at-maturity. Analysis was fitted to otolith data presented in Huntsman et al. (2018) from one warm (site 2) and two cool (site 1 and site 3) streams. The vertical and horizontal dotted lines (*Maturity* in the legend) represent the identified age- and length-at-maturity for Rio Grande cutthroat trout. The extension of immature growth beyond the age- and size-at-maturity inflection point represents the conceptual growth of a mature fish under the unlikely scenario that no energy is partitioned away from somatic growth

TABLE 2 Matrices relating observation and state processes of Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) demographic rates. Apparent survival (ϕ), state transitions (Ψ) and recapture probability (p) are shown for immature (I) and mature (M) states

True State (t)	True State ($t + 1$)		
	Immature	Mature	Dead
Immature	$\phi_I(1 - \Psi_{I-M})$	$\phi_I\Psi_{I-M}$	$1 - \phi_I$
Mature	0	ϕ_M	$1 - \phi_M$
Dead	0	0	1

True State (t)	Observed State (t)		
	Seen as Immature	Seen as Mature	Not Seen
Immature	p	0	$1 - p$
Mature	0	p	$1 - p$
Dead	0	0	1

growth temperature for RGCT in summer (Figure S2; 15.3°C, Zeigler et al., 2013). Lastly, we included a temperature and density interaction effect on our transition parameter because elevated competition for a limited foraging base can exacerbate the elevated metabolic costs caused by warming temperatures on ectotherms (Crozier, Zabel, Hockersmith, & Achord, 2010).

Model selection was performed by the indicator variable approach (Hooten & Hobbs, 2015; Kuo & Mallick, 1998), where each regression coefficient (β) besides sampling interval was multiplied by a binary indicator variable ($w \sim \text{Bernoulli}(0.5)$) to select the best model structure for demographic and detection parameters of our CMR analysis. The indicator variable approach can then be used to calculate the posterior model probabilities based on the frequency of the MCMC outputs of different sequences of the indicator variables. Additionally, we used 95% credible intervals to evaluate the effects of covariates on demographic and detection parameters. Vague priors were used for all regression parameters (Normal (0,100) Tr(-5, 5)), with σ as a Uniform (0, 10). Lastly, we used the same JAGS criteria (e.g. number of iterations) for the CMR analysis as the Lester growth analysis.

Site- and time-specific vital rates were estimated from the most parsimonious model structure identified by model selection. Thus, site- and season-specific predictor variables (e.g. degree days, effective density) were used to predict apparent survival of both immature and mature RGCT states, as well as transition rates between states based on Equations 5 and 6. Note that random site effects from Equations 5 and 6 (ϵ_{ϕ_i} and ϵ_{Ψ_i}) allow for site-specific estimates of demographic rates, even if an intercept model is found most parsimonious. Annual survival and annual transition probabilities from spring 2016 to spring 2017 were calculated based on our seasonal vital rate estimates between our sampling occasions (e.g. survival between spring and summer sampling occasions in 2016 = $E_{(\text{spring}-\text{summer } 2016)}$) using the following equations (Powell, 2007):

$$\phi_{\text{Annual}} = \phi_{(\text{spring}-\text{summer } 2016)} * \phi_{(\text{summer}-\text{fall } 2016)} * \phi_{(\text{fall } 2016-\text{spring } 2017)} \quad (10)$$

$$\Psi_{\text{Annual}} = 1 - [(1 - \Psi_{(\text{spring}-\text{summer } 2016)}) * (1 - \Psi_{(\text{summer}-\text{fall } 2016)}) * (1 - \Psi_{(\text{fall } 2016-\text{spring } 2017)})] \quad (11)$$

We also estimated demographic rates for each season on a monthly scale by similarly using site- and season-specific predictor variables within Equations 5 and 6 to predict survival and transition probabilities for our observed sampling intervals. We converted seasonal survival estimates to monthly survival by raising seasonal survival to the power of the reciprocal number of months during that sampling interval (e.g. 2 months between spring and summer with survival of $0.90 = 0.90^{(1/2)} = 0.95$ survival probability for 1 month). Seasonal transition probabilities were converted to monthly probabilities using the following equation:

$$\Psi_{\text{Monthly}} = 1 - (1 - \Psi_{\text{Seasonal}})^{\frac{1}{t}} \quad (12)$$

where seasonal estimates of transition probability (Ψ_{Seasonal}) were converted to monthly probabilities based on the number of months (t) during that seasonal sampling interval.

3 | RESULTS

3.1 | Lester growth model and maturity

The Lester growth model found evidence of a temperature effect (DIC = 2093.9) on immature RGCT growth rates (h in Equation 1) and lengths- and ages-at-maturity compared to a constant model (DIC = 2,297.3), although specific parameter estimates were highly variable. Growth rates of immature RGCT were slower at the cool sites (mean $h = 31.8$ mm, 95% credible intervals = 27.8 to 37.1 mm; sites 1 and 3) than the warm site (mean $h = 49.4$ mm, 95% credible intervals = 39.0 to 68.5 mm; site 2). Growth trajectories (length-at-age) for RGCT were also slower in the cool sites compared to the warm site (Figure 2). Age-at-maturity for the cool sites was estimated to be 4.0 years (95% credible intervals = 2.6–6.1 years), which corresponded to lengths-at-maturity of approximately 140 mm (95% credible intervals = 90–227 mm). Maturity was reached at a younger age (mean = 2.0 years, 95% credible intervals = 0.3–3.9 years) and a smaller size (mean length = 120 mm, 95% credible intervals = 44–270 mm) at the warm site compared to the cool sites (Figure 2), although difference could not be stated with certainty due to overlapping 95% credible intervals.

3.2 | Mark-recapture and demographic rates

We tagged a total of 1578 RGCT but reduced that number to 1552 for analysis due to mortality caused by sampling. Of those 1552 tagged RGCT, 749 individuals were recaptured at least once throughout the study (Table 1). The highest number of tagged ($n = 441$) and recaptured ($n = 241$) fish were encountered in a cool

site (site 6). The lowest number of tagged ($n = 34\text{--}44$) and recaptured RGCT ($n = 15\text{--}20$; Table 1) were encountered at two warm sites (sites 4 and 8) and the one site invaded by brown trout (site 3).

Model selection by the indicator variable approach revealed that recapture probability was constant over time but varied by size-classes (Table 3). Bayesian weight for the constant model was 66.9% for immature and 69.3% for mature RGCT (Table 3). Mean recapture probability was lowest for RGCT in the immature state (mean = 0.43, 95% credible intervals = 0.28 to 0.60), and the highest estimate of recapture probability was for RGCT in the mature state (mean = 0.62, 95% credible intervals = 0.50 to 0.74).

The effects of covariates on apparent survival varied by RGCT state within our sampling sites. Apparent survival was best explained by an intercept model for immature RGCT (Bayesian weight = 61.3%; Table 3). A model with temperature and effective density had the highest Bayesian weight for mature RGCT survival (Bayesian weight = 52.5%, Table 3). Apparent survival of mature RGCT increased with effective density (mean $\beta_{\text{Density}} = 0.62$, 95% credible interval = 0.24 to 1.05) and decreased with warming temperatures ($\beta_{\text{Temp}} = -0.88$, 95% credible interval = -1.46 to -0.35 ; Figure 3).

Estimates of apparent survival varied between states, among sites and between states within sites. Apparent survival was generally lower for immature than mature RGCT at cool sites and highest for immature RGCT at warm sites (Table S2, Figure 4). One of the four warm sites (site 2) was an exception where annual apparent survival estimates were higher for mature than immature RGCT (Table S2). The brown trout invaded site (site3) was also the one exception among the four cool sites, where immature RGCT had higher survival than mature RGCT (Table S2). Seasonal estimates of apparent survival among cool sites were also lowest within the invaded stream for immature and mature RGCT (Figure 4). The lowest survival rates of both immature and mature RGCT among warm sites were also observed from the same site (site 4, Figure 4). Comparisons between years within the same season showed little differences across cool sites, but the two warm sites that share a confluence (sites 4 and 8) showed the greatest differences in mature RGCT survival (Figure 4). Specifically, mature RGCT apparent survival was higher from summer to fall in 2016 (mean φ_A from site 4 = 0.92 and 95% credible intervals = 0.84 – 0.98, site 8 mean = 0.92 and 95% credible intervals = 0.85 – 0.97) than 2017 for both sites (mean φ_A from site 4 = 0.72 and 95% credible intervals = 0.60 – 0.82, mean site 8 = 0.80 and 95% credible intervals = 0.70–0.88; Figure 4, Table S2).

Transition probability from an immature to mature state was affected by both effective density and degree days. The indicator variable approach to model selection indicated that transition probability from immature into the mature state (Ψ_{I-M}) was best explained by an effective density and degree day effect with 48.2% of the model weight (Table 3). As effective density increased, the probability of transitioning into a mature state decreased ($\beta_{\text{Density}} = -0.47$, 95% credible interval = -0.83 to -0.13 ; Figure 5). Additionally,

TABLE 3 Best model structure for Rio Grande cutthroat (*Oncorhynchus clarkii virginalis*) trout multistate model parameters identified by the indicator variable method. “Immature-Mature” represents immature to mature transition probability

Model	Structure	Bayesian weight
Immature survival	Intercept	61.3
	Temperature	17.0
	Effective density	6.8
	Discharge	5.6
	All other combinations	<5.0
Mature survival	Temperature + Effective density	52.5
	Temperature + Effective density + Discharge	19.3
	Temperature + Discharge	16.6
	All other combinations	<5.0
Immature-Mature	Degree days + Effective density	48.2
	Degree days	27.7
	Degree days + Effective density + Degree days:Effective density	5.3
	All other combinations	<5.0
	Immature recapture probability	Intercept
	Discharge	28.1
	All other combinations	<5.0
Mature recapture probability	Intercept	69.3
	Discharge	26.0
	All other combinations	<5.0

as the number of degree days increased, so did the probability that immature RGCT transitioned into a mature state ($\beta_{\text{Degree}} = 0.94$, 95% credible interval = 0.57 to 1.33; Figure 5).

4 | DISCUSSION

We investigated how extrinsic (discharge and temperature) and intrinsic (density) constraints shape the life history of RGCT through demographic rates. Our analyses indicated that RGCT from cool and high-density sites possessed a relatively “slow” pace of life, where RGCT reached ages-at-maturity at an older age and larger size. Opposite our expectations, we found no statistical evidence for a relationship between apparent survival of immature RGCT and intrinsic or extrinsic environmental conditions. However, mortality rates of mature RGCT did increase with temperature, providing evidence consistent with life-history theory that suggests the pace at which species complete their life cycle (slow-fast life-history continuum) is partly affected by age-class specific mortality (Perrin & Rubin, 1990).

There are multiple environmental and biological factors that influence the rate at which different life stages are reached and

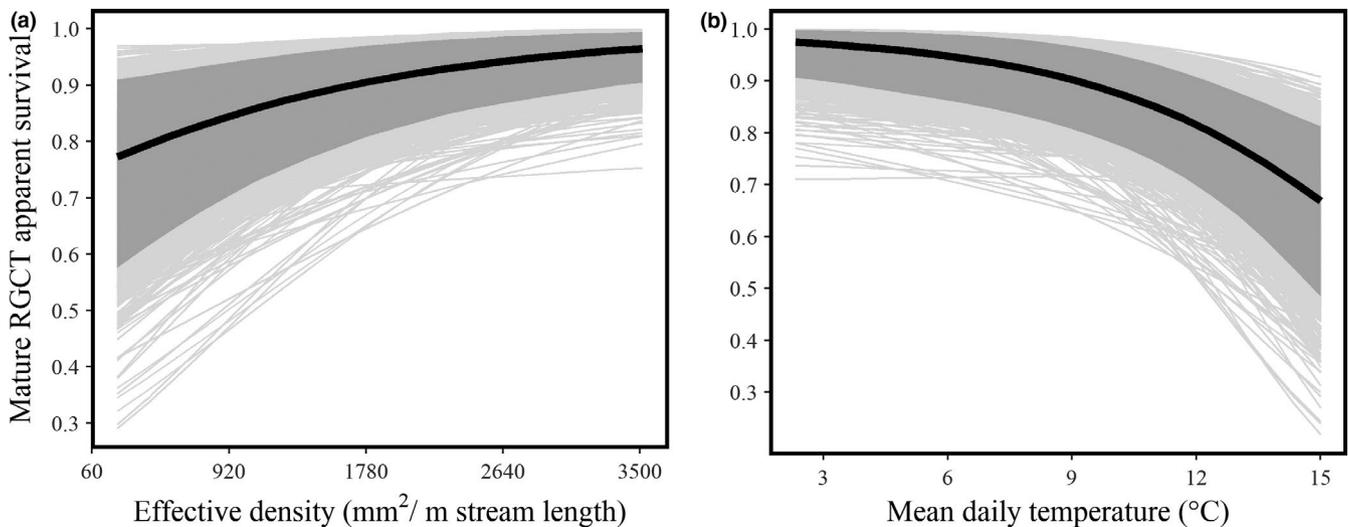


FIGURE 3 Apparent survival (ϕ) of mature Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) as a function of covariates in northern New Mexico streams. Apparent survival was best explained by effective density (see Equation 9) and mean daily temperature. The shaded area represents the 95% credible interval, the dark black line is the mean, and light grey lines are each individual posterior estimate of the demographic parameter. Survival probabilities are reported as monthly rates. Note that the rates are independent of season and represent predictions from the best supported model

life-history traits expressed (Moore, Riesch, & Martin, 2016). Warm and highly productive habitat often favour organisms with “faster” life-history trait expression (e.g. *r*-selected, faster individual growth, exponential population growth, early maturity and senescence) while relatively cool and low productivity environments are often inhabited by individuals expressing a “slower” life-history strategy (e.g. *K*-selected, slower growth, population carrying capacity; Zhu et al., 2014; Cayuela et al., 2016; Moore et al., 2016). Although 95% credible intervals overlapped, model selection provided some evidence that stream temperatures affected the age and size by which RGCT reached maturity. In particular, slower growing RGCT from cool sites were 97% more likely to reach an older age and 81% more likely to reach a larger size-at-maturity than RGCT from warmer sites, where the larger sizes at maturity presumably coincided with greater fecundity (Cowley, 2008; Perrin & Rubin, 1990). The opposite patterns were observed for RGCT from warm sites, where a slightly earlier age- and smaller size-at-maturity was found, but this state was reached at a younger age than RGCT from cool sites. The otolith data used for this analysis did not have sex information, which could have affected our results if sex ratios strongly differed between warm and cool sites because males typically mature faster than females (Downs, White, & Shepard, 1997). A common reason for differences in sex ratios is angling pressure because male trout are more susceptible to angling (Downs et al., 1997; Meyer, Schill, Elle, & Lamansky, 2003). However, we sampled headwater streams that received low fishing pressure and thus would be less affected by skewed sex ratios. Although the temperature-maturity patterns in this study were observed from relatively limited data (otoliths from 1 cool and 2 warm sites without sex-specific information), they are consistent with patterns in survival-reproduction trade-offs commonly documented in other species (Abrams, 1991; Tavecchia et al., 2005).

We found evidence for a strong negative density effect on the rate at which immature RGCT transitioned into a mature state, contrary to expectations for species like RGCT that are at the periphery of all cutthroat trout distributions (Guo, Taper, Schoenberger, & Brandle, 2005; Zeigler et al., 2019). Similarly, Huntsman and Petty (2014) found peripheral brook trout (*Salvelinus fontinalis*) populations within an Appalachian watershed were regulated and argued that this was likely an indirect effect of a regulated source of immigrants rather than density dependence on local demographic performance. Here, each of our RGCT populations is isolated above barriers, indicating our density-maturity relationship was driven by local demographic processes. The optimal age- and length-at-maturity for a species is shaped by factors that affect growth and mortality in fishes (Perrin & Rubin, 1990). Ward et al. (2017) found both climatic variables and density dependence directly affected growth rates of the juvenile rainbow trout (*O. mykiss*) life stage (*h* in the Lester growth model), a parameter the authors found among the most important in determining the rate at which maturity was reached. This likely also explains our density-maturity relationship since we found no evidence that RGCT survival rates decreased with increased density and RGCT from warm sites had faster immature growth and reached maturity quicker than RGCT from cool sites.

We expected strong temperature and discharge relationships with immature RGCT survival, given our site selection was designed to span abiotic conditions (i.e. temperature and flow) commonly observed to influence survival in trout populations (Bassar, Letcher, Nislow, & Whiteley, 2016; Kanno, Letcher, Coombs, Nislow, & Whiteley, 2014; Letcher et al., 2015; Xu, Letcher, & Nislow, 2010). However, this was not observed in our study and may be due to a few potential mechanisms. None of our sites consistently exceeded the 30-day upper incipient lethal temperatures established in a laboratory setting for juvenile RGCT (21.7°C; Zeigler et al., 2013), and

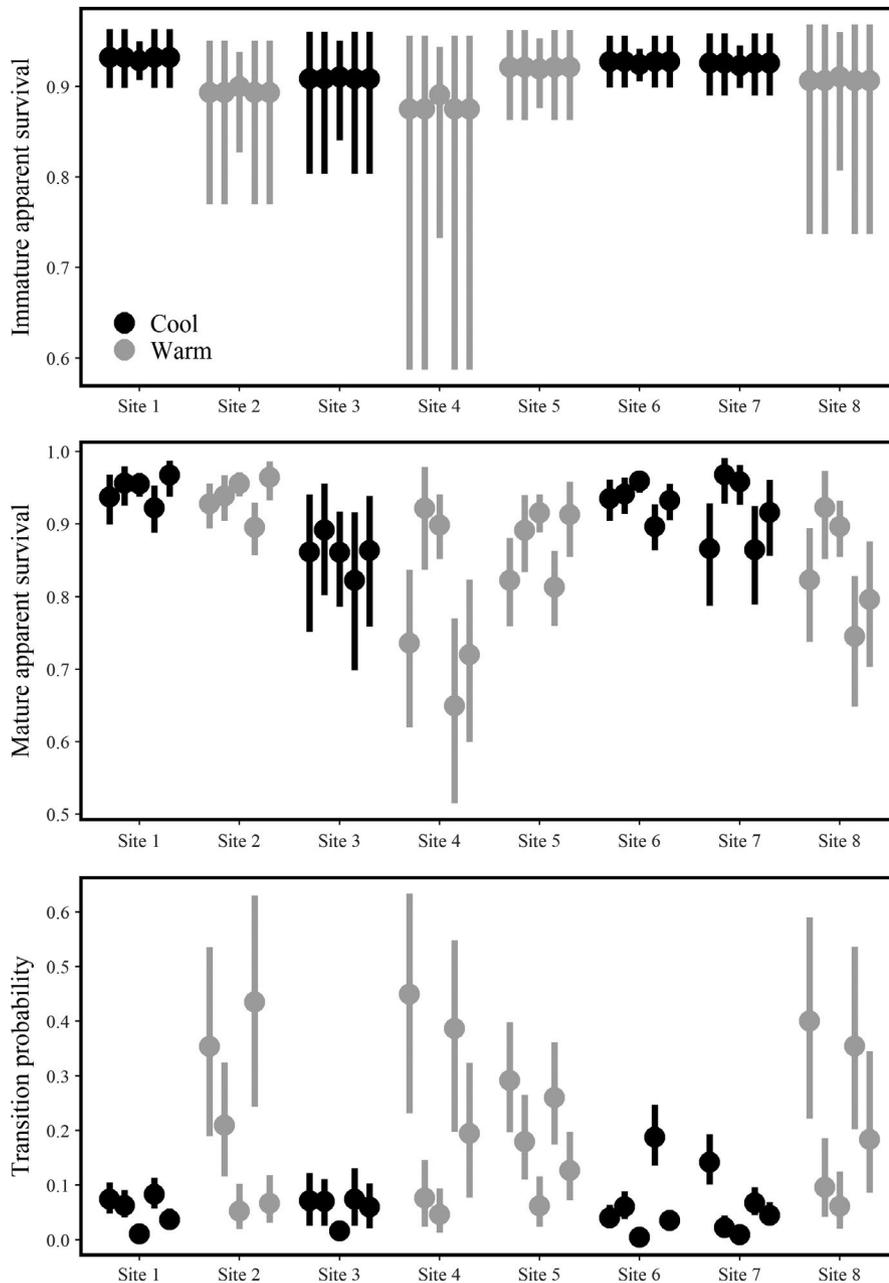


FIGURE 4 Monthly vital rate estimates for Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) from northern New Mexico streams. Filled circles are estimated means with 95% credible intervals as vertical lines. The monthly rates are reported from left to right within each sampling site for the following seasons: spring–summer 2016, summer–fall 2016, fall 2016–spring 2017, spring–summer 2017 and summer–fall 2017

each site undoubtedly possesses thermal micro-refugia that presumably influences trout demography (Petty, Hansbarger, Huntsman, & Mazik, 2012) and development (Huntsman et al., 2018). Also, the two wet years (relative to other years from this decade; Figure S1) in which our sampling occurred may have reduced the effects of temperature and especially flow on the survival of immature RGCT within our study sites. Interestingly, Zeigler et al. (2019) found temperature and flow to have a relatively subdued effect on RGCT persistence, especially when considered in the context of biological invasions. Expanding our sampling effort spatially and especially temporally would help properly characterise the effects that environmental conditions may have on immature RGCT survival.

Our results demonstrated a strong temperature effect on mature RGCT survival. The negative relationship between temperature and mature, but not immature, RGCT survival may reflect the greater

metabolic costs that larger compared to smaller-bodied ectotherms incur as temperatures increase (Brown, Gillooly, Allen, Savage, & West, 2004). Although physiologically stressful temperatures provide a plausible explanation for our survival patterns among RGCT maturity states, a more parsimonious explanation suggests RGCT from our warmest sites had a faster pace of life and earlier senescence. This is further supported by the faster rate by which RGCT reached maturity within warmer sites (this study), mature RGCT survival decreased within warmer sites even though temperatures were below critical thermal limits (this study), and RGCT reached a smaller asymptotic body size with a faster instantaneous growth rate when occupying warm streams (Huntsman et al., 2018). Furthermore, the temperature–adult survival relationships observed in this study may be confounded with the onset of spring spawning in our RGCT populations. Elevated rates of mortality are expected following

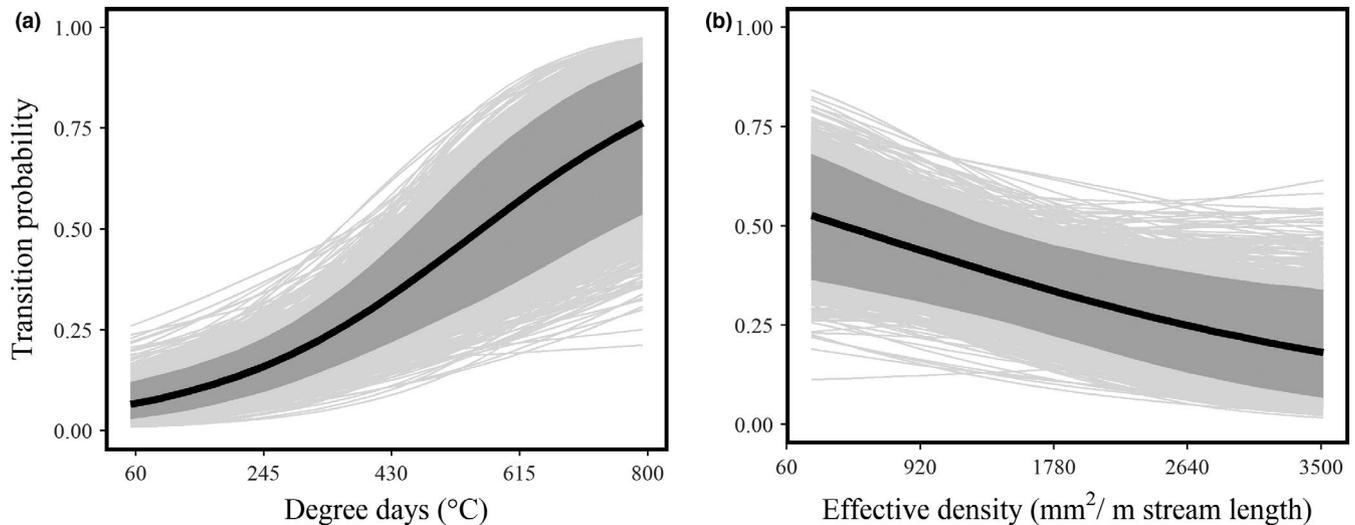


FIGURE 5 Mature state transition probability (Ψ) of Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) as a function of environmental covariates in northern New Mexico streams. Transitions were best explained by effective density (see Equation 9) and degree days. The shaded area represents the 95% credible interval, the dark black line is the mean, and light grey lines are each individual posterior estimate of the demographic parameter. Transition probabilities are reported as monthly rates

reproduction due to the substantial energy investment required for this life-history event (Stearns, 1989), and may also be responsible for the lower survival rates in RGCT during the spring–summer sampling interval in our study. Lastly, we cannot ignore the potential for lower RGCT apparent survival to reflect a greater emigration rate rather than mortality rate in the warmer sites. However, further information would be needed to separate true mortality from emigration in our study.

Apparent survival of mature RGCT in this study showed a surprising relationship with density, opposing expectations of a negative feedback mechanisms affecting population growth found in other trout populations (Grossman et al., 2010; Grossman & Simon, 2019; Huntsman & Petty, 2014). Although inverse density dependence at low densities (*i.e.* Allee effects) is possible under certain ecological scenarios (Courchamp, Clutton-Brock, & Grenfell, 1999), they likely do not explain the direct correlation between mature RGCT survival and density. A more likely explanation is that the observed density dependence may be the result of RGCT habitat selection behaviour within our study sites. Specifically, the lower apparent survival of RGCT in low-density habitats may actually reflect greater emigration rates of RGCT out of the study site as opposed to higher mortality rates. Thus, if the low-density study sites are characterised as poor RGCT habitat (*e.g.* no fish cover) and the RGCT are transients moving through the sampling site, then this might explain the positive density effect on RGCT survival we observed. Unfortunately, we have no information pertaining to RGCT movement or home range size within our study sites to determine how likely this might explain the positive density dependence observed at these sites.

One of the greatest threats to cutthroat trout persistence is invasion by non-native species (Bakevich et al., 2019; Muhlfeld et al., 2017; Roberts, Fausch, Hooten, & Peterson, 2017; Zeigler et al., 2019). Native trout commonly occupy cooler habitats than

non-native trout introduced to the intermountain West (Wenger et al., 2011). Some evidence also suggests that competitive abilities of fishes are tied to thermal tolerance ranges (Taniguchi, Rahel, Novinger, & Gerow, 1998), potentially giving RGCT a competitive advantage over non-native fishes when found within cold high-elevation streams. However, McHugh and Budy (2005) observed that brown trout always dominated interactions with Bonneville cutthroat trout (*O. c. utah*) regardless of stream temperature, even though fish distributions were commonly segregated by temperature. Interestingly, we found brown trout to be the most common salmonid encountered within our invaded study site, which was also among the coldest sites sampled during this study (site 3). While competition with non-native trout often affects multiple life-history events of native fishes (*e.g.* foraging, habitat selection, direct predation; Benjamin & Baxter, 2010; McHugh & Budy, 2005; Seiler & Keeley, 2009; Shemai, Sallenave, & Cowley, 2007; Yard, Coggins, Baxter, Bennett, & Korman, 2011), transition rates were equally high from our invaded site as the other cool sites. This suggests brown trout may have had a relatively minor effect on the rate by which RGCT reached maturity at our invaded site.

Although not an objective of this study, our results provide evidence that brown trout may affect RGCT survival. The presence of non-native trout species, as well as factors associated with their invasion potential within a native RGCT stream (*e.g.* barrier presence), was determined to be the most pressing threats to RGCT persistence now and in the future (Zeigler et al., 2019). We found mature survival rates to be lowest within the invaded site (site 3) compared to all other RGCT populations sampled for this study besides site 4. Interestingly, mature RGCT annual survival rates from all other cool sites were two times greater than that observed for RGCT within the invaded site, indicating a deviation from the temperature-survival pattern determined in this study. Evidence of the

direct impact of brown trout on cutthroat trout survival has been variable, where cutthroat trout survival can be significantly lower in the presence of brown trout (Budy, Thiede, & McHugh, 2007), no strong brown trout effects on cutthroat trout survival may occur (McHugh & Budy, 2005), and stronger effects within immature than mature cutthroat trout states (Al-Chokhachy & Sepulveda, 2019) have all been documented. Although we have evidence for a brown trout effect on RGCT survival, a direct test of these effects would require a greater number of invaded streams be studied to confirm such an effect. Regardless, non-native competitors have been identified by numerous researchers as among the most serious threats to persistence of native fishes, with concerns only heightened by the threat of a changing climate (Benjamin & Baxter, 2010; Muhlfeld et al., 2014, 2017; Roberts et al., 2017; Wenger et al., 2011; Zeigler et al., 2019).

We used a space-for-time study design in an attempt to describe demography of trailing edge RGCT populations in response to environmental constraints. Abnormally high stream flows during our study limited our ability to infer the effects of stream drying on RGCT population dynamics. Ultimately, the lack of “drought” conditions during our study may highlight the potential limitations of using a space-for-time study design when attempting to describe variability in life-history traits. It is reasonable to assume that RGCT from intermittent streams would be more severely affected by drought conditions than RGCT from perennial streams. Our results suggest that wet years result in relatively benign flow effects on RGCT survival and development rates, regardless of the streams’ hydrologic history. However, we cannot ignore the importance of stream flows on other salmonid life-history characteristics (recruitment), or the impacts of true drought conditions on trout vital rates and productivity (Hakala & Hartman, 2004; Kovach et al., 2016; Letcher et al., 2015; Nislow, Sepulveda, & Folt, 2004). Consequently, space-for-time study designs may not adequately capture population-specific sensitivities to climatic conditions during relatively rare events (Pickett, 1989) and longer time series are needed to properly identify threats to RGCT persistence.

5 | CONCLUSIONS

In this study, density and temperature affected demographic rates of RGCT populations in northern New Mexico. Although survival decreased with temperature, RGCT matured faster when sites were warmer and suggests that plasticity in trait expression is a life-history characteristic which may assist the most southern cutthroat trout to persist. As trailing edge populations continue to be spatially constrained by an ever-shrinking area of suitable habitat due to warming and invasion of non-native trout, the presence of a portfolio of diverse life-history traits may provide the adaptive capacity of RGCT to persist in an uncertain future. Thus, it would be informative to consider life-history diversity among RGCT populations when assessing current and future risks and how conserving this diversity may improve their resiliency to these threats.

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AUTHOR CONTRIBUTIONS

BMH, AJL and CAC conceived and designed the investigation. BMH, AJL and CAC performed field and/or laboratory work. BMH and FA analysed the data. BMH, AJL, CAC and FA wrote the paper.

DATA AVAILABILITY STATEMENT

Data will be made available in science base. <https://www.sciencebase.gov/catalog/item/55366d88e4b0b22a15807cb6>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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