Check for updates

Received: 26 October 2022 | Revised: 1 February 2023 | Accepted: 27 February 2023

DOI: 10.1002/rra.4122

RESEARCH ARTICLE

WILEY

Climate change impacts on native cutthroat trout habitat in Colorado streams

Chenchen Ma[1] | Ryan R. Morrison[1] | Daniel C. White[1] | James Roberts[2] | Yoichiro Kanno[3,4]

[1]Civil and Environmental Engineering, Colorado State University, Fort Collins, Colorado, USA

[2]U.S. Geological Survey, Great Lakes Science Center – Lake Erie Biological Station, Huron, Ohio, USA

[3]Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

[4]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

Correspondence
Ryan R. Morrison, Civil and Environmental Engineering, Colorado State University, Fort Collins, CO, USA.
Email: ryan.morrison@colostate.edu

Funding information
U.S. Geological Survey

Abstract

Headwater streams support vital aquatic habitat yet are vulnerable to changing climate due to their high elevation and small size. Coldwater fish are especially sensitive to the altered streamflow and water temperature regimes during summer low flow periods. Though previous studies have provided insights on how changes in climate and alterations in stream discharge may affect habitat availability for various native cutthroat trout species, suitable physical habitats have not been evaluated under future climate projections for the threatened Greenback Cutthroat Trout (GBCT) native to headwater regions of Colorado, USA. Thus, this study used field data collected from selected headwater streams across the current distribution of GBCT to construct one-dimensional hydraulic models to evaluate streamflow and physical habitat under four future climate projections. Results illustrate reductions in both predicted streamflow and physical habitat for all future climate projections across study sites. The projected mean summer streamflow shows greater decline (−52% on average) compared to the projected decline in mean August flow (−21% on average). Moreover, sites located at a relative higher elevation with larger substrate and steeper slope were projected to experience more reductions in physical habitat due to streamflow reductions. Specifically, streams with step-pool morphologies may experience grater changes in available habitat compared to pool-riffle streams. Future climate change studies related to coldwater fish that examine spatial variation in flow alteration could provide novel data to complement the existing literature on the thermal characteristics. Tailoring reintroduction and management efforts for GBCT to the individual headwater stream with adequate on-site monitoring could provide a more holistic conservation approach.

KEYWORDS

aquatic habitat, climate change, headwater streams, hydraulic modelling, Rocky Mountains, trout

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *River Research and Applications* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Headwater streams, defined as first- and second-order channels, account for nearly 80% of total river length in the United States (US) (E. Wohl, 2017). In mountainous regions, such as the Rocky Mountains, headwater streams are typically characterized by relatively high gradients with predominately gravel and cobble substrate (Jarrett, 1992; E. Wohl, 2010). They also serve as critical habitat for threatened endemic fish species, as well as food sources for fish and other aquatic and riparian organisms (Colvin et al., 2019; Meyer et al., 2007; Schlosser, 1995; Wipfli & Baxter, 2010).

The size and watershed position of headwater streams makes them especially sensitive to alterations in hydroclimatic conditions caused by changing climate (Beniston, 2003). Climate change in mountainous regions is of particular concern because seasonal snowpack, an important component of regional water supplies, is declining in the western United States (Pederson, Betancourt, & McCabe, 2013; Scalzitti, Strong, & Kochanski, 2016). Furthermore, warmer temperatures in winter and spring are shifting precipitation patterns from snow-dominant to rain-dominant hydrologic regimes in mountainous regions (Klos, Link, & Abatzoglou, 2014). As evapotranspiration increases and precipitation regimes shift because of warming climate, annual mean discharge will likely decrease (Berghuijs, Woods, & Hrachowitz, 2014; Furey, Kampf, Lanini, & Dozier, 2012; Hammond & Kampf, 2020; Jefferson, 2011; Milly & Dunne, 2020; White, Morrison, & Wohl, 2022), resulting in lower base flows in late summer months and a reduction of stream habitat to an extent that could significantly affect coldwater fish (Bradford & Heinonen, 2008; Watts, Grant, & Safeeq, 2016).

The native cutthroat trout species in the Southern Rocky Mountains have been declining with habitat loss from land-use changes, non-native trout species invasion, and water abstraction from human activities over the last 150 years (Roberts, Fausch, Hooten, & Peterson, 2017). Although increases in summer temperature might benefit age-0 cutthroat trout in the highest-elevation Colorado streams due to a longer growth period (Coleman & Fausch, 2007), diminishing streamflow in summer could amplify the already stressful environment for native cutthroat trout (Mantua, Tohver, & Hamlet, 2010; Roberts et al., 2017).

One of the native trout in the Southern Rocky Mountains is the Greenback cutthroat trout (*Oncorhynchus clarkii stomias*), which is the only salmonid native to the mountain and foothill waters of the South Platte River basin in Colorado (Metcalf et al., 2012). The greenback cutthroat trout (GBCT) were abundant in the late 19th century (Young, Harig, Rosenlund, & Kennedy, 2002), but their populations declined rapidly during the last century due to mining pollution, agriculture, harvesting for commercial sale, and non-native trout invasions (Young et al., 2002; Young & Harig, 2001). The GBCT are listed as threatened under the Endangered Species Act, and their present management focuses on establishing additional populations by propagating and reintroducing fish originating from the Bear Creek in the Arkansas River basin in central Colorado, which was the last remaining genetically pure, self-reproducing population of GBCT (Metcalf et al., 2012). Thus, identifying habitat characteristics suitable for reintroduction and long-term persistence of GBCT populations is paramount to the successful recovery of this threatened species. However, uncertainties exist regarding how long-term habitat suitability is influenced in the changing climate and how it varies over space.

Previous studies show that populations of native cutthroat trout species in the western United States will likely be harmed due to hydrologic impacts of climate change (e.g., Kovach et al., 2016; Roberts, Fausch, Peterson, & Hooten, 2013; Williams, Haak, Neville, & Colyer, 2009). Existing native cutthroat trout populations in the western United States are already restricted to short headwater stream fragments due to habitat loss and non-native trout invasions (Harig & Fausch, 2002). The effects of climate change could further stress native cutthroat trout populations, as described by Roberts et al. (2017), who found that the combined outcome of climate change and non-native cutthroat trout invasion could extirpate 39% of the total Colorado River cutthroat trout populations and put another 37% of the populations at risk of extirpation in the Southern Rocky Mountains. Furthermore, a systematic review of 42 studies across nine countries that have quantified relationships between trout populations and temperature or streamflow suggested that climate-induced changes in hydrology are expected to have more influential consequences for trout than the summer and fall temperatures (Kovach et al., 2016), highlighting the importance of hydrologic changes likely to occur in headwater streams. The aforementioned studies demonstrate that native cutthroat trout populations are already reduced to small headwater streams, where climate-driven alterations in streamflow can affect the population persistence due to decreases in flow. Moreover, they also emphasized the importance of taking multiple factors (e.g., stream-specific physical characteristics) into account when assessing climate impacts on coldwater trout habitat instead of only focusing on the thermal characteristics. Thus, evaluating the effects of climate change on native cutthroat trout populations could be improved by including possible changes in habitat driven by reduced streamflow.

Numerous studies have reported the negative impacts of reduced streamflow on fish species, including the loss of habitat (Bradford & Heinonen, 2008; Garbe, Beevers, & Pender, 2016; Hakala & Hartman, 2004; May & Lee, 2004), lowered water quality (Benejam, Angermeier, Munné, & García-Berthou, 2010; Guyette & Rabeni, 1995), and increased predation risk as a result of reduced water depth and velocity (Bradford & Heinonen, 2008; Harvey & Stewart, 1991; Heggenes & Borgstrom, 1988), which can lead to decreased population recruitment and survival (Jonsson & Jonsson, 2009). These studies highlight the importance of understanding the effects of climate-driven changes in streamflow on hydrological parameters that directly impact suitable habitat for trout. Because measuring all environmental conditions of interest over a timeframe that is adequate for robust statistical data analyses of the seasonal variations of hydrological parameters is particularly difficult (Meier & Reichert, 2005), utilizing hydraulic models to simulate various scenarios can be advantageous for quantifying climate change effects on trout habitat.

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

1.1 | Research objectives

Evaluating the effects of climate-induced streamflow changes on available habitat that support GBCT can be important for future management and preservation efforts. Previous work has included quantitative analysis to evaluate the minimum habitat requirements under climate change for native cutthroat trout species in the Rocky Mountain (Roberts et al., 2013, 2017; Williams et al., 2009). However, these studies quantified climate change effects at a broad scale relying mostly on GIS derived data, which might not be representative of individual sites that are candidates for reintroduction of GBCT. Hence, this study focuses on gathering more detailed stream morphologic and hydraulic measurements with the goal of evaluating the impact of future climate on instream habitat for threatened GBCT. To support this goal, we seek to answer the following research questions: (1) To what degree will GBCT habitat be reduced in headwater streams; and (2) Are there specific morphological or other characteristics that make headwater streams more susceptible to habitat loss? To answer these research questions, we used projections of future streamflow and one dimensional (1-D) hydraulic models to evaluate the current and future habitat metrics for GBCT (see Figure 1). Furthermore, we statistically related loss of habitat to relevant morphological stream attributes to determine site locations less suitable for GBCT persistence or future reintroduction.

2 | METHODS

2.1 | Study site characteristics

Twelve study sites located in the headwater regions along the Front Range in Colorado were selected with elevation ranging from 2156 to 3487 m (Figure 2 and Table 1). These sites were selected as high priority GBCT conservation sites because they either support self-reproducing populations of this subspecies established via past reintroduction (Bear Creek, Herman Gulch, and Zimmerman Creek) or are candidates for future reintroduction (Harry Crockett, Colorado Parks and Wildlife, personal communication). Current efforts to restore GBCT populations focus on reintroducing them in headwater streams of their native South Platte basin, and reintroductions occur upstream of physical barriers (e.g., waterfalls and artificial barriers) to protect reintroductions populations from invasions by non-native trout species (Fausch, Rieman, Dunham, Young, & Peterson, 2009). Our 12 study sites represent habitats where most self-reproducing populations of GBCT occur in the foreseeable future.

The climate in the Front Range varies with altitude from an annual average of 100 cm of precipitation and 2°C at the highest elevations (~4000 m), to 40 cm and 10°C along the mountain front (~1500 m) (Wohl, 2001). High flows in the rivers throughout the Front Range are caused by convective summer storms occurring mainly in July and August, or from snowmelt during late May and June

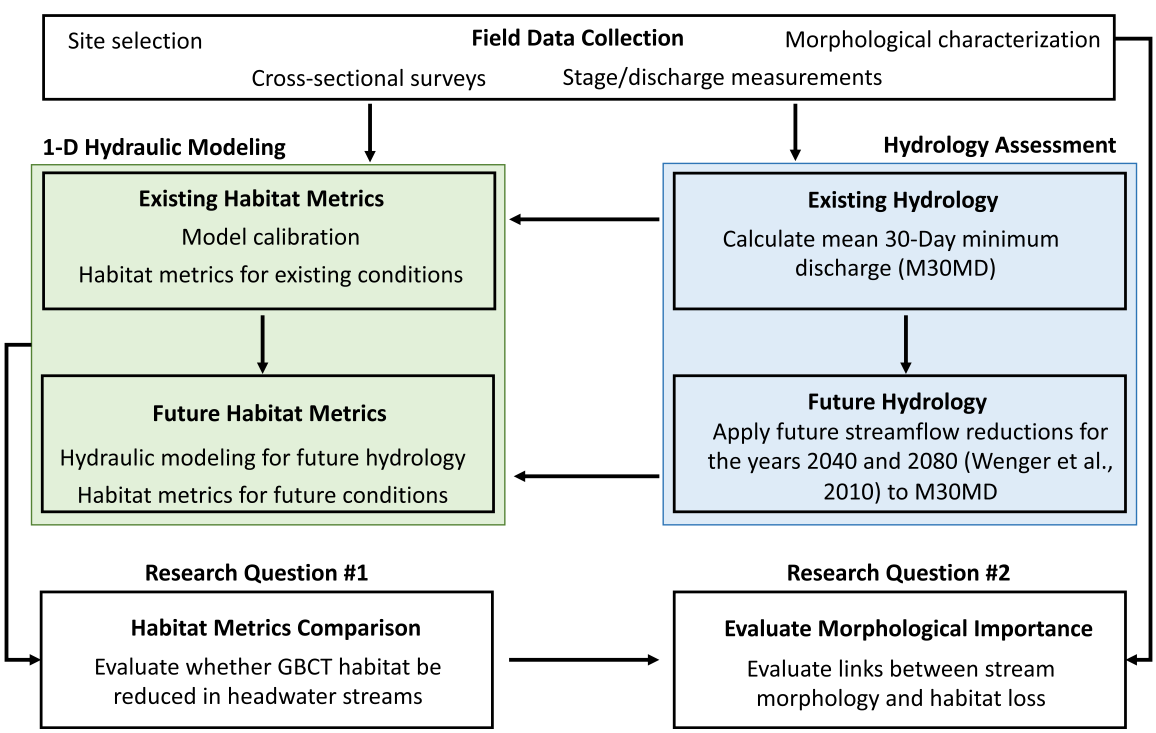

FIGURE 1 Illustration of the research approach used in the study of climate impacts on greenback cutthroat trout in headwater regions of the Rocky Mountain Front Range, Colorado, USA. Boxes in green indicate steps associated with hydraulic modelling and boxes in blue indicate steps associated with the hydrology assessment. [Color figure can be viewed at wileyonlinelibrary.com]

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

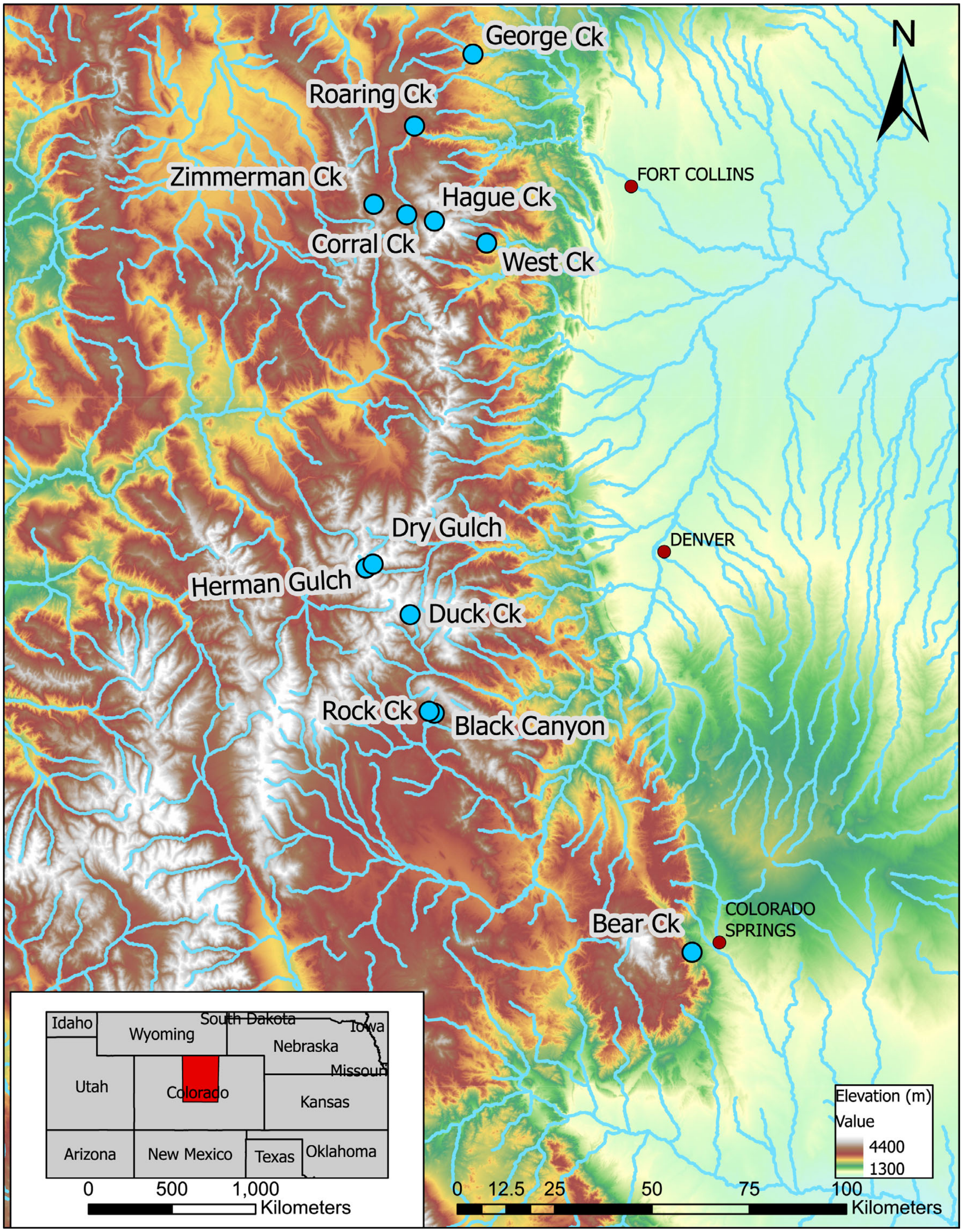

FIGURE 2 Geographic location of each study site throughout the Rocky Mountain Front Range, Colorado, USA. [Color figure can be viewed at wileyonlinelibrary.com]

that may last for 2 to 3 weeks (E. E. Wohl, 2001). Forest ecology in the Front Range is dependent on elevation and can be categorized into alpine tundra of grasses and dwarf tress lying between elevations of 3480 to 4300 m; subalpine forest of spruce and fir down to 2800 m; and montane forest of mixed aspen, conifers and other deciduous down to the transition to steppe vegetation at about 1700 m (Wohl, 2001).

2.2 | Channel surveys

Channel geometry surveys were conducted for each site throughout the summer of 2019 using a stadia rod and Leica conventional sight level. The surveyed site length, which was selected to be representative of the morphological conditions at each site based on visual inspections, varied between 27 and 75 m depending on the specific

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Study site characteristics from current and high priority restoration Greenback Cutthroat Trout (GBCT) streams in the Southern Rocky Mountains.

Site	Latitude	Longitude	Particle size (mm)			Slope	Elevation	Aspect	Site length	Mean Bankfull depth	Mean channel top width	Montgomery and Buffington classification	Drainage area
	Degrees N	Degrees E	D25	D50	D84	(m/m)	(m)		(m)	(m)	(m)		(km^2)
Bear Creek	38.799	−104.949	2.3	3.8	10.8	0.07	2201	SW	27	0.23	2.8	Step Pool	11.7
Black Canyon Creek	39.363	−105.670	2.8	5.4	91.3	0.05	2933	SE	33	0.33	2.4	Step Pool	10.3
Corral Creek	40.520	−105.822	5.3	75.9	186.5	0.03	3036	NE	55	0.5	3.9	Step Pool	14.5
Dry Gulch	39.705	−105.895	56.1	104.7	173.1	0.04	3298	SE	44	0.36	3.8	Step Pool	8.0
Duck Creek	39.591	−105.745	24.0	42.5	119.3	0.11	3650	NW	29	0.3	2.5	Cascade	2.0
George Creek	40.889	−105.699	8.7	50.6	86.6	0.02	2367	SE	35	0.42	3.2	Pool Riffle	37.3
Hague Creek	40.498	−105.678	19.0	30.2	54.3	0.007	3008	NW	75	0.6	10.2	Pool Riffle	13.4
Herman Gulch	39.719	−105.898	47.0	84.1	157.1	0.05	3306	NE	30	0.37	3.8	Step Pool	8.1
Roaring Creek	40.770	−105.731	24.7	51.8	138.9	0.02	2677	SE	36	0.38	5.3	Pool Riffle	23.9
Rock Creek	39.368	−105.686	27.4	41.8	76.2	0.02	2925	SE	42	0.37	3.8	Pool Riffle	16.0
West Creek	40.458	−105.534	24.7	41.3	200.1	0.07	2502	SW	34	0.56	9.3	Step Pool	24.3
Zimmerman Creek	40.541	−105.865	3.4	4.5	8.7	0.006	3202	NE	27	0.25	1.8	Pool Riffle	1.1

Note: These 12 sites were studied to determine the current and possible future hydraulic conditions of streams throughout the entire distribution of GBCT.

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

morphology of the stream (Table 1). For instance, low gradient sites (e.g., Hauge Creek, Table 1) required longer survey lengths so that we could capture the variability in morphological features, such as pools and bars. A total of 10 cross sections for each site were surveyed, and the location of the thalweg, water surface elevation, and bank elevations were noted. The cross-section locations aligned with changes in channel morphology (e.g., cross-sections collected across riffles, pools, etc.). The total streamwise site length was the cumulative distance between surveyed cross sections. Channel width was calculated as the distance between right and left bank locations; average bankfull depth was obtained by averaging the weighted bankfull depth, which is calculated by subtracting elevation of each surveyed cross-section point from the averaged right and left bankfull elevations. The particle distribution for each site was measured within a riffle representative of general stream characteristics following the Wolman pebble count method (Wolman, 1954). Between 50 and 100 particles were sampled at roughly 0.5-m intervals across the channel. The elevation of each site was obtained using GPS data collected in the field using a Garmin handheld unit (model eTrex 22x), and the average slope for each site was calculated as the difference in upstream and downstream water surface elevations over the total surveyed distance. The aspect for each site was derived using a Geographic Information System (Google Earth). Finally, the morphological classification of each site was assigned using the Montgomery and Buffington channel classification system (Montgomery & Buffington, 1997). A photographic representation of the morphological classifications identified during field work are shown in Figure 3.

2.3 | Streamflow data collection

2.3.1 | Discharge time series

Time series data of water levels and atmospheric pressure were obtained using data loggers (Onset HOBO U20L) that were placed in stable stream location in each study site. Absolute pressure (P_a) was recorded in the channel at 30-min intervals from June 2019 to September 2020. A logger was also installed adjacent to the channel in open air to correct for atmospheric pressure (P_{atm}). A time series of flow depth, (h) was calculated using the gauge pressure ($P_{abs}-P_{\mathrm{atm}}$) as follows:

$$h=\frac{P_{abs}-P_{atm}}{\rho_{\mathrm{w}} g} \tag{1}$$

Here, h is flow depth over the sensor (m), P_{abs} is the hydrostatic pressure (P_a), P_{atm} is the recorded atmospheric pressure (P_a), ρ_{w} is water density (1000 kg/m^3), and g is acceleration due to gravity (9.81 m/s^2).

For each study site, a rating curve was developed using measured discharge data and the calculated depth at the time when the discharge was measured. Discharge was measured using an Acoustic Doppler Velocimeter (Sontek FlowTracker 2). The rating curve equation was generated using the power trendline between the relative head and stream discharge, and the derived equation for each site was then applied to calculate stream discharge using the computed relative head for each 30 min interval. Rating curves for Duck Creek and Zimmerman Creek could not be developed because accurate atmospheric data were not available at these two sites. However, morphological data from Duck Creek and Zimmerman Creek were used the principal components analysis analyses (see below).

2.3.2 | Mean 30-day minimum discharge

A mean 30-day minimum discharge (M30MD) was computed between June 14 to September 30 using a 30-day rolling average for the years 2019 and 2020. For example, the first 30-day average value was calculated using discharge values between June 14 and July 14th. The next 30-day average was calculated between June 15 and July

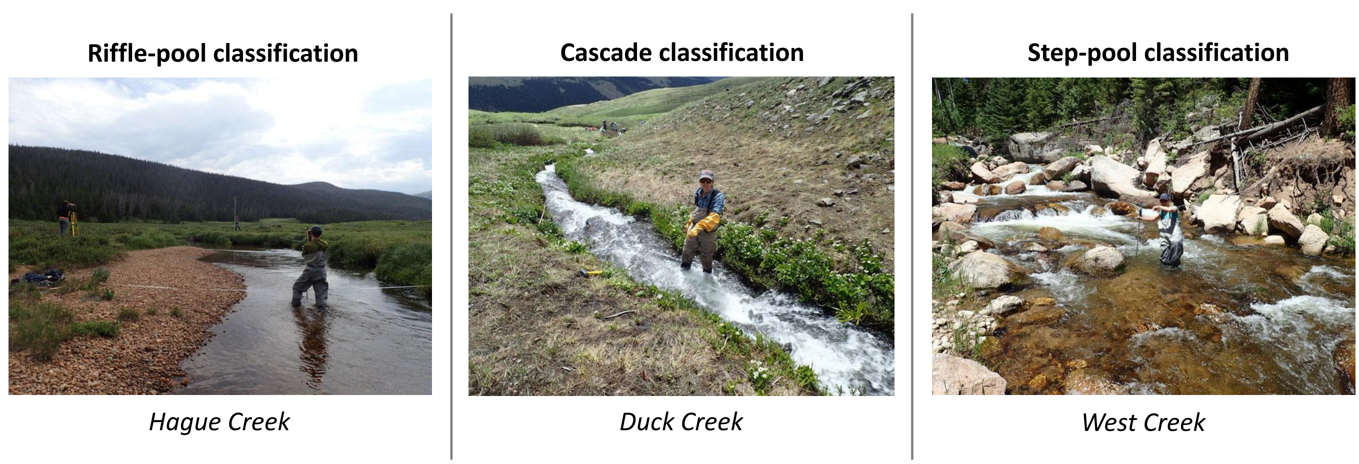

FIGURE 3 Photographic representations of the three stream morphologies identified throughout our study sites. From left to right in the above figure, the morphology classifications include riffle-pool streams, cascade streams, and step-pool streams. The site name of each classification is indicated below the photographs. [Color figure can be viewed at wileyonlinelibrary.com]

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

15, and this calculation was repeated through September 30. The final 30-day average discharge values was calculated between September 30 and October 30, and the minimum value from the rolling average was picked for the year. This metric is particularly important for cold water fish habitat during summertime low flow because water depth provides habitat and cover, particularly for larger trout (Harig & Fausch, 2002; Heggenes & Borgstrom, 1988). The mean value for M30MD was calculated as the average of the 2019 and the 2020 M30MD values.

2.3.3 | Future streamflow projections

Projected future streamflow reductions for the years 2040 and 2080 were obtained from the Western US Stream Flow Metrics database (Wenger, Luce, Hamlet, Isaak, & Neville, 2010). The forecasted changes to streamflow were based on daily simulations using a variable infiltration capacity (VIC) macroscale hydrologic model. A VIC model is a physically based and fully distributed model that solves surface water balance, which has been widely adopted in the western United States to forecast hydrologic changes (Wenger et al., 2010). Streamflow for historical conditions (1977–2006) and future years of 2040 (mid central time period, centered around 2040s) and 2080 (end of century time period, centered around the 2080s) were downloaded directly from the database based on the stream network IDs that aligned with GPS coordinates of each study site.

The flow variables selected from the database that were relevant to this study include the mean summer flow (MS; the average of daily discharge between June 1 and September 30) and the mean August flow (MAUG; the average of daily August discharge and generally representative of baseflows in headwater streams) (Coleman & Fausch, 2007; Wenger et al., 2010). Both mean August and mean summer flows were included in the analyses because of the hydrologic durations of each. August projections are important because by late summer only baseflows are present in headwater streams. Mean summer flows, on the other hand, include the full range of snowmelt runoff and baseflow conditions. If both baseflows and runoff flows are reduced due to climate change, this could cause a loss of available habitat over longer periods of time compared to only reductions in baseflow following snowmelt runoff. To estimate hydrologic responses to future climate conditions at each site, the 2040 and 2080 MS and MAUG percent reductions (e.g., the difference between historical and 2040/2080 discharges) were applied to the measured M30MD discharge at each site.

2.4 | One-dimensional hydraulic modelling

2.4.1 | Model development and calibration

Field data collected at each site were used to develop one-dimensional (1-D) hydraulic models. The US Army Corps of Engineering Hydrologic Engineering Center's River Analysis System (HEC-RAS) version 6.1 model was chosen for the 1-D models (US Army Corps of Engineers, 2016). HEC-RAS is a robust hydraulic modelling software that is widely used to for engineering, geomorphic, and ecohydraulic applications. Because 1-D models were used in this study, all hydraulic results, such as velocity, were depth-averaged at each cross-section and represented only the streamwise (downstream) direction, and therefore do no capture lateral or secondary flow patterns that may create beneficial habitat for fish.

The basic process for using field data to develop each HEC-RAS model included the following steps: (1) the stream geometry was created using the survey cross-section data for each site, including the elevation and distance information within each cross section and between cross sections; (2) the bank elevations were approximated at each cross section based on the survey notes and identifiable breaklines between the channel and floodplain topography; (3) model boundaries were chosen to represent normal-depth flow conditions; and (4) discharge values were selected to match measured discharged.

As previously stated, at least 10 surveyed cross-sections were measured in the field, and these cross-sections formed the basis for the channel geometry in HEC-RAS. Measured and predicted discharge values were simulated under steady flow conditions (e.g., a single flow value was modelled for each simulation rather than a time series of discharges). The models used a mixed flow regime to account for supercritical and subcritical hydraulic conditions, and steady flow boundary conditions were selected for numerical stability based on observed flow characteristics.

Accuracy of Manning's roughness coefficient can significantly influence the calculated hydraulic characteristics in a natural channel (Ferguson, 2007). To calibrate the Manning's roughness coefficient for each model, the root mean square error (RMSE) was calculated using differences in water surface elevation between simulated and observed conditions for a range of roughness values. The calibration process for each site used a single discharge that was collected during the channel geometry surveys. The Manning's roughness coefficient with the smallest RMSE value was selected as the calibrated value for modelling additional discharges.

2.4.2 | Simulated flows

Discharges simulated in each HEC-RAS model include: (1) the calibrated discharge, which was measured during cross-sectional surveys; (2) M30MD, which is the measured mean 30-day minimum discharge from the rolling averages between June 14 and September 30; (3) 2040MS and 2040MAUG discharges; and (4) 2080MS and 2080MAUG discharges.

2.4.3 | Modelled habitat characteristics

HEC-RAS modelling values for water velocity (m/s), channel wetted perimeter (m), and maximum flow depth (m) were used to assess changes in habitat quality. The site-averaged and cross-sectional

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

habitat values were examined for each site. Although specific habitat metrics necessary for GBCT population persistence have not been documented, the selected variables (i.e., velocity, wetted perimeter, and depth) are important for other trout species (Bjornn & Reiser, 1991). Specifically, trout compete for drifting food in summer (Nakano, Kitano, Nakai, & Fausch, 1998) and velocity determines drift food rate and capture efficiency by trout (Piccolo, Hughes, & Bryant, 2008). Water depth is critical as larger trout need deeper pools as cover (Heggenes, Northcote, & Peter, 1991). Plus, wetted perimeter is an index of total surface habitat area, and its reduction in summer affects trout survival and growth (VerWey, Kaylor, Garcia, & Warren, 2018; Xu, Letcher, & Nislow, 2010).

2.5 | Morphological indicators of habitat change

Principal components analysis (PCA; Jolliffe, 2002) was used to summarize dominant morphological variation among sites and investigate whether the magnitude of physical habitat change differs among sites in the future climate. The PCA reduces the dimensionality of a dataset and seeks a more parsimonious representation of a complex data set based on collinearity of variables (Jolliffe, 2002; Jolliffe & Cadima, 2016). Variables used in the PCA included elevation, average slope, D50 (median substrate grain size), D84 (84 percentile substrate grain size), averaged channel top width, and average channel depth (Table 1). Latitude was initially included in the PCA but was removed because latitudinal gradient was too small relative to the overall range of GBCT. These variables were then reduced to two main principal components (PCs), which are linear functions of the original variables that are uncorrelated with each other and can maximize variance (Jolliffe & Cadima, 2016). Relationships between PCs and the percent change in simulated physical habitats under different future climate projections were then analysed with simple linear regression to quantify which sites would experience the greatest changes in habitat characteristics under future climate projections. The PCA was conducted using R statistical software (version 4.1; R Core Team, 2021), the "prcomp" function in the stats package (R Core Team, 2021) and the "ggbiplot" function in the ggplot2 package (Wickham, 2016) package. Statistical significance was set at $\alpha = 0.05$.

3 | RESULTS

3.1 | Streamflow under future climate projections

The percent reductions in MS flow obtained from the Western US Stream Flow Metrics database were −7% to −53% for 2040 and −18% to −80% for 2080. Similarly, the percent reduction in MAUG flow obtained from the database were −7% to −37% for 2040 and −3% to −46% for 2080.

Mean summer discharges were projected to decrease more than mean August discharges (Table 2). In addition, reductions from 2080 scenarios for both mean summer and August illustrate greater decreases in streamflow compared to the 2040 future climate projection scenario. It is worth noting that the percent reductions in streamflow show a large variation among sites under both climate projection

TABLE 2 Summary table for calibrated, mean 30 day minimum, and projected mean summer and mean August flows for 2040 and 2080 from 10 current and high priority restoration Greenback Cutthroat Trout streams in the Southern Rocky Mountains of Colorado.

		Mean 30-day min discharge (m^3/s)			Year 2040		Year 2080	
					Mean summer discharge	Mean august discharge	Mean summer discharge	Mean august discharge
Site	Calibrated discharge (m^3/s)	2019	2020	Average	% change	% change	% change	% change
Dry Gulch	0.44	0.042	0.084	0.063	−53%	−10%	−80%	−15%
Corral Creek	0.74	0.005	0.001	0.003	−45%	−11%	−79%	−16%
Herman Gulch	0.19	0.027	0.047	0.037	−52%	−12%	−77%	−18%
West Creek	0.21	0.143	0.159	0.151	−36%	−32%	−69%	−44%
Hague Creek	0.91	0.013	0.018	0.016	−33%	−37%	−64%	−46%
Roaring Creek	0.13	0.047	0.048	0.047	−32%	−6%	−48%	−10%
Bear Creek	0.018	0.01	0.007	0.009	−21%	−21%	−38%	−36%
Black Canyon	0.068	0.021	0.004	0.012	−19%	−7%	−28%	−10%
Rock Creek	0.15	0.019	0.008	0.014	−15%	−3%	−23%	−3%
George Creek	0.08	0.023	0.011	0.017	−7%	−7%	−18%	−10%

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

scenarios (2040 MS ranges from −53% to −7%; 2040 MAUG ranges from −3% to −37%; 2080 MS ranges from −80% to −18%; and 2080 MAUG ranges from −3% to −46%).

It is important to note that the measured streamflow values at each site were not the same as contemporary estimates from the Western US Stream Flow Metrics database (See Study Limitations section).

3.2 | Simulated habitat metrics

Mean summer projections experienced greater habitat reductions compared to mean August projections for both 2040 and 2080 future climate scenarios (Table 3 and Figure 4). Across all the sites, the habitat metrics decreased between −2% and −23% for 2040MS and −2% and −46% for 2080MS simulations. Single-site habitat metric reductions tended to be similar across all metrics such that velocity, wetted perimeter, and depth had similar percent reductions (e.g., reductions in velocity, wetted perimeter, and depth at Dry Creek were −19%, −20%, and −23%, respectively; Table 3). The greatest decreases in all three simulated physical habitats were found under the 2080 mean summer future climate projection (Figure 4), which was expected since this scenario included the largest reduction in streamflow. Some sites had greater variabilities in the simulated physical habitat (e.g., West Creek and Roaring Creek) than others. Furthermore, variation was observed among sites as shown in each boxplot (Figure 4), indicating the magnitude of physical habitat reduction is site-specific under future climate projections. The calibrated Manning's roughness coefficients varied between 0.055 to 0.45 with a RMSE ranging from 0.017 to 0.10 (see Table S1).

Some calibrated Manning's roughness coefficients found in this study are much larger than maximum values suggested elsewhere (e.g., Chow, 1959; Coon, 1998). However, these results are consistent with previous studies suggesting mountain streams with higher gradient have considerably high values of the Manning's coefficient (Reid & Hickin, 2008; Yochum, Bledsoe, David, & Wohl, 2012; Yochum, Comiti, Wohl, David, & Mao, 2014).

3.3 | Responses of physical habitat to projected flow reductions

Results from the PCA (Figure 5) showed that approximately 68% of the variation among sites can be explained by the first two principal components (PC1 = 38.7%, PC2 = 29.2%). Contributing drainage area, average channel width, and average bankfull depth were positively correlated with PC1. Conversely, site elevation, substrate size (e.g., D50 and D84) and stream slope were negatively correlated with PC2.

There was a significant relationship between the PC2 and percent change in simulated physical habitats for both 2040 ($R^2 = 0.64$–0.79, $p < 0.01$) and 2080 ($R^2 = 0.38$–0.78, $p < 0.01$–0.058) mean summer climate projections (Figures 6 and 7). Because PC2 had high negative loadings of average slope, elevation, and substrate sizes, these results indicated that sites located at higher elevations with steeper slopes and larger substrates would experience greater changes in available habitat. Furthermore, step-pool morphology streams would experience greater changes and more variability in available habitats compared to streams with pool-riffle morphology (Figures 5 and 6). No significant relationships were found between PC1 and reductions in physical habitats for 2040 or 2080 climate projections ($R^2 = 0$–0.31; $p = 0.31$–0.96) (Figures 5 and 6). In contrast, the magnitude of habitat change was much smaller for mean August (results can be found in Figures S1 and S2).

4 | DISCUSSION

4.1 | Implications for GBCT conservation

Conservations efforts for GBCT will be influenced by changes in streamflow and available habitat across a range of hydrologic time periods. The results from the projected streamflow reductions (Table 3 and Figure 4) demonstrate that substantial reductions occur in the mean summer projections but not in the mean August projections. This is likely because the mean summer flow projections capture large reductions in overall snowpack, snowmelt runoff, and earlier runoff timing that will occur in the southern Rocky Mountain (Clow, 2010; Harpold et al., 2012; Pederson et al., 2013), whereas the August flow characterizes only baseflow which is not projected by the model to decrease to the same extent. Declining summer streamflow is also reported in the Central Rocky Mountains (Leppi, DeLuca, Harrar, & Running, 2012; Rood et al., 2008). The more modest decreases in mean August flow are likely due to the buffering effects of the groundwater storage and discharge in the mountain watersheds providing resilience to climate-driven hydrologic changes (Liu, Gebremeskel, De Smedt, Hoffmann, & Pfister, 2004; Rumsey, Miller, Susong, Tillman, & Anning, 2015; Somers & McKenzie, 2020). However, it is worth noting that the decreases in mean August flows (baseflows) even with smaller percent reductions could be more stressful to GBCT because survival and growth of salmonids are negatively affected by low summer flows in headwater streams (Harvey, Nakamoto, & White, 2006; Uthe, Al-Chokhachy, Shepard, Zale, & Kershner, 2019; Xu et al., 2010).

Furthermore, decreases in streamflow have been reported to substantially increase water temperatures (van Vliet et al., 2012). This interaction is likely to impair water quality (Ducharne, 2008) but could benefit recruitment of young-of-the-year fish in high-elevation streams where cold temperature and short summer growing seasons currently limit their recruitment (Coleman & Fausch, 2007). Impacts of climate change varies among sites, but up to 20% reductions in velocity, wetted perimeter, and flow depths were projected by 2040 and 40% reductions in habitat were projected in 2080 based on changes in summer streamflow (Table 3). These habitat reductions could have detrimental impacts on trout populations.

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 3 Mean habitat metric reductions for each modelled scenario across 10 current and high priority restoration Greenback Cutthroat Trout streams in the Southern Rocky Mountains of Colorado.

	2040MS			2040MAUG			2080MS			2080MAUG		
Site	Velocity	Wetted perimeter	Maximum depth	Velocity	Wetted perimeter	Maximum depth	Velocity	Wetted perimeter	Maximum depth	Velocity	Wetted perimeter	Maximum depth
Dry Gulch	−19%	−20%	−23%	−3%	−3%	−4%	−32%	−45%	−44%	−4%	−4%	−5%
Corral Creek	−16%	−14%	−16%	−3%	−2%	0%	−39%	−47%	−34%	−4%	−3%	−5%
Herman Gulch	−19%	−20%	−23%	−3%	−4%	−4%	−29%	−39%	−40%	−5%	−5%	−6%
West Creek	−14%	−10%	−13%	−12%	−9%	−12%	−34%	−25%	−32%	−18%	−13%	−17%
Hague Creek	−16%	−8%	−11%	−18%	−9%	−12%	−39%	−19%	−26%	−23%	−12%	−17%
Roaring Creek	−12%	−7%	−9%	−1%	−1%	−1%	−20%	−16%	−20%	−2%	−2%	−3%
Bear Creek	−6%	−9%	−9%	−4%	−9%	−9%	−12%	−14%	−16%	−11%	−13%	−16%
Black Canyon	−7%	−6%	−5%	−3%	−2%	−5%	−6%	−9%	−12%	−7%	−6%	−5%
Rock Creek	−3%	−4%	−7%	0%	−1%	−1%	−7%	−7%	−10%	0%	−1%	−1%
George Creek	−2%	−2%	−2%	−1%	−2%	−2%	−2%	−6%	−7%	−2%	−2%	−4%

Note: All columns show percent changes compared to average mean 30-day minimum values.

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

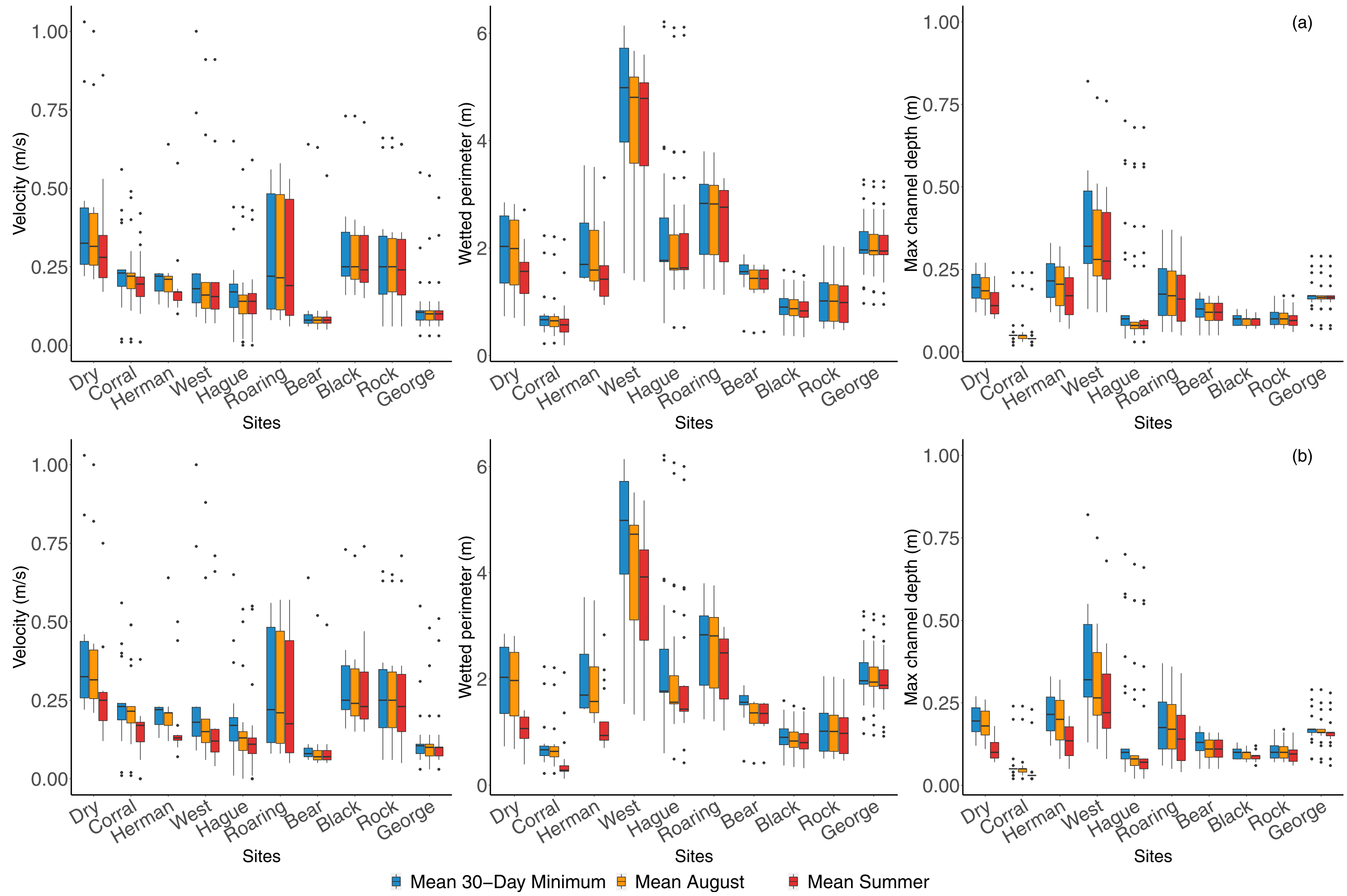

FIGURE 4 Results for simulated physical habitat (velocity, wetted perimeter, and max channel depth) under mean summer and mean August climate change projections for (a) 2040, and (b) 2080. The barplot lines represent median, 25% and 75%, and 10% and 90% values. The dots above and below the bars are outlier data. These results indicate modelled physical habitat characteristics across 10 study sites in the headwater regions of the Rocky Mountain Front Range, Colorado, USA. [Color figure can be viewed at wileyonlinelibrary.com]

For instance, stream salmonids show density-dependent body growth patterns in summer (Huntsman, Lynch, & Caldwell, 2021; Vøllestad & Olsen, 2008), and reduced wetted perimeter would result in a smaller carrying capacity of headwater habitats via summer flow reductions. In addition, larger trout require depth as cover in small streams (Penaluna, Dunham, & Andersen, 2021; Sotiropoulos, Nislow, & Ross, 2006). Heggenes et al. (1991) reported that cutthroat trout larger than 9 cm total length selected stream habitats with depths >25 cm, and maximum channel depths are already or projected to be below this threshold in many study streams. Finally, slower velocity would reduce drift food availability, which is the primary food source for stream salmonids in summer (Owens & Keeley, 2022; Uthe et al., 2019). Optimal foraging velocity of stream salmonids during base flow conditions range between 20 and 40 cm/s (Morita, Sahashi, & Tsuboi, 2016; Nislow, Folt, & Parrish, 1999), which again fall within the velocity range projected in the current and future climate scenarios for the study sites. Taken together, this analysis shows that the magnitude of available habitat alterations projected in this study could affect persistence of native cutthroat trout populations in high-elevation Colorado streams.

It was found that climate change impacts on available habitat would vary among sites, with higher-elevation sites, characterized by steeper slopes and larger substrates, being more likely to experience greater degrees of available habitat changes owing to future flow reductions (Figures 6 and 7). This result aligns with elevation-dependent climate impacts found in the Rocky Mountains and other mountain regions that are experiencing rapid climate-driven changes, such as flow reductions (e.g., Papadaki et al., 2016; Pederson et al., 2013; Tague & Dugger, 2010). Although the scope of this research was not to investigate the specific mechanisms of changes in available habitat across morphological stream types, steeper streams with larger substrate at higher elevations may be more sensitive to flow reductions because of the already shallow flows that tend to be present in high-gradient streams compared to low-gradient streams for a given discharge (Vezza, Parasiewicz, Spairani, & Comoglio, 2014). Under large reductions of flows, this typically results in drying of step habitats and physical isolation of remaining pool habitats, where trout congregate and demographic rates such growth and survival are negatively impacted (Hakala & Hartman, 2004; Penaluna et al., 2021). Ultimately, flow reduction impacts on trout populations depends on

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

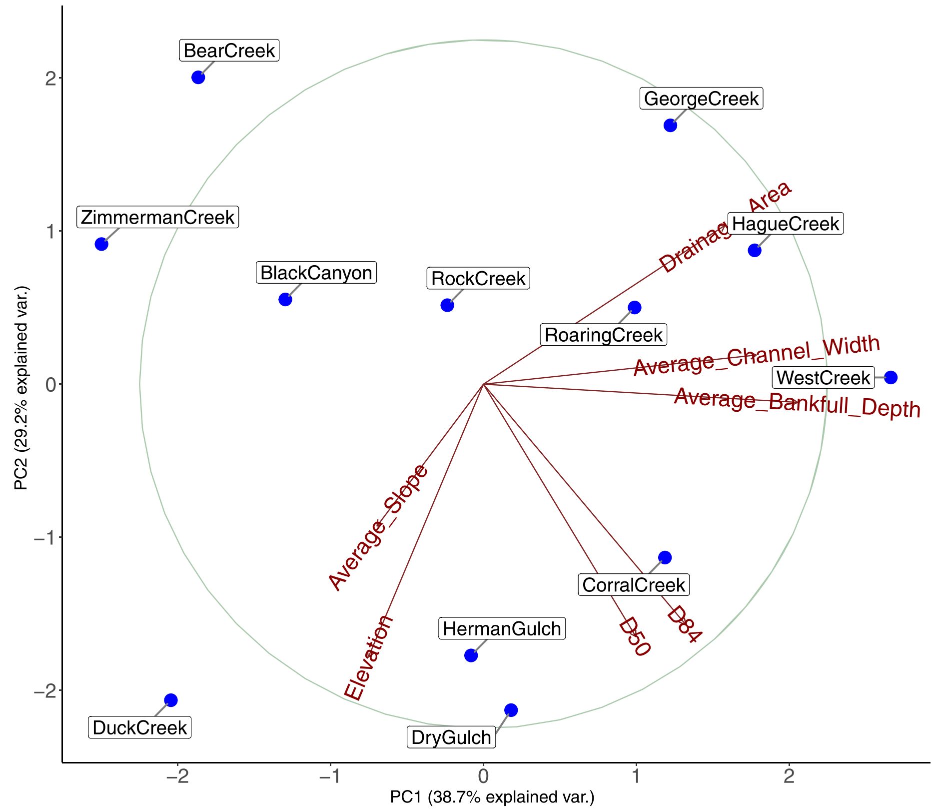

FIGURE 5 Plot of the first two axes of the principal component analysis for 12 study sites in the headwater regions of the Rocky Mountain Front Range, Colorado, USA. Sites are shown in dots and variables in lines. [Color figure can be viewed at wileyonlinelibrary.com]

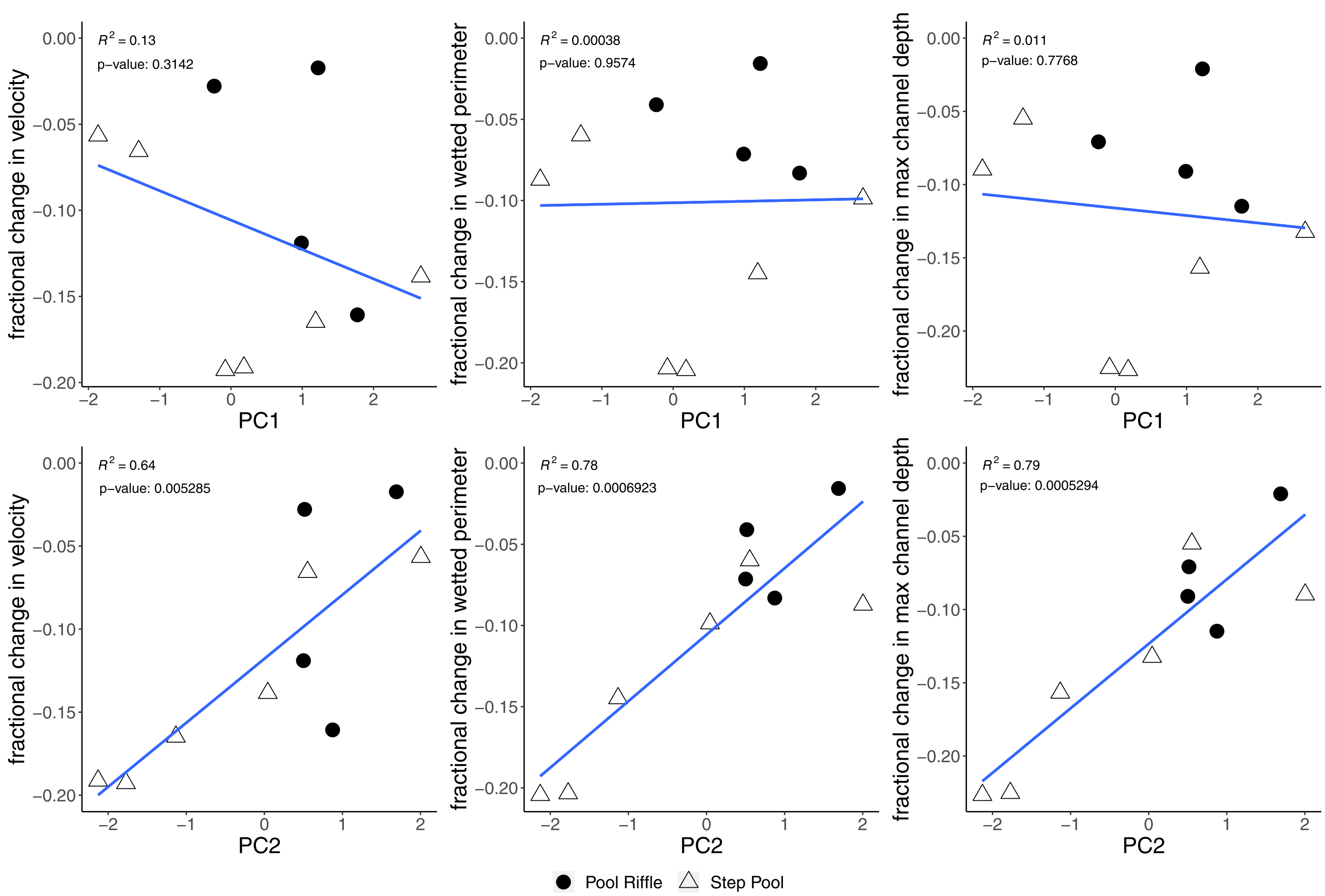

FIGURE 6 Relationships PC1, PC2, and simulated reductions in physical habitats under 2040 mean summer projections for 10 study sites in the headwater regions of the Rocky Mountain Front Range, Colorado, USA. [Color figure can be viewed at wileyonlinelibrary.com]

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

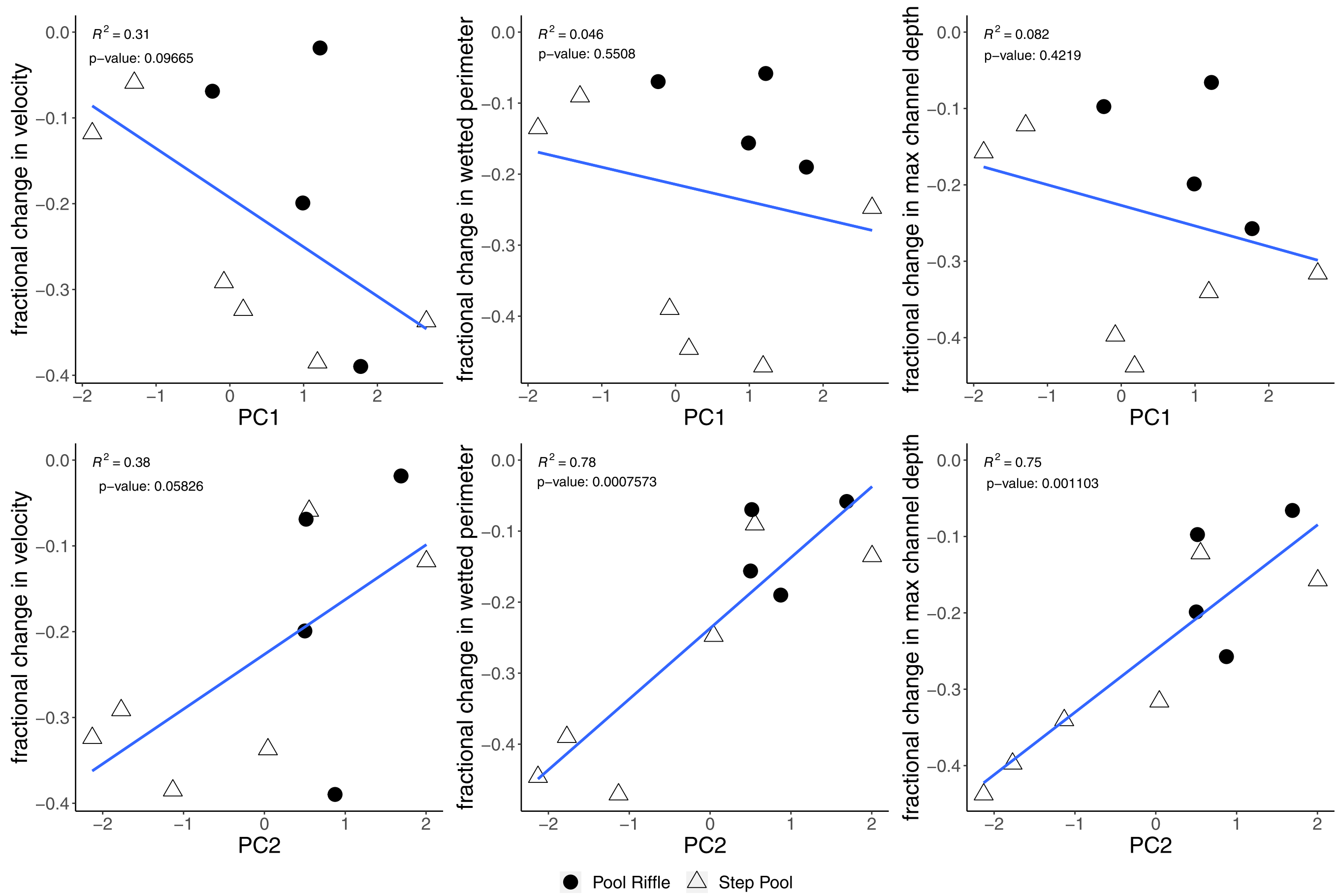

FIGURE 7 Relationships PC1, PC2, and simulated reductions in physical habitats under 2080 mean summer projections for 10 study sites in the headwater regions of the Rocky Mountain Front Range, Colorado, USA. [Color figure can be viewed at wileyonlinelibrary.com]

availability of pools, which may differ by habitat morphology (cascade vs. step-pool vs. riffle-pool morphology) (Rosenfeld & Boss, 2001; Vezza et al., 2014). Since high-gradient streams with large substrate tend to be located at higher elevations (though not always), these sites, which also will have less contributing area to capture snowmelt runoff, may have habitat that is most impaired in future climates. In addition, since GBCT has already been confined to higher elevations (Cook, Rahel, & Hubert, 2010), the loss of habitat in steep, high-elevation streams will exert more stress on the GBCT population that are often outcompeted by non-native trout.

In addition, conservation of native trout in the intermountain Western USA has frequently occurred in high-elevation, small headwaters because of the need for physically isolating their populations from invasion by non-native trout species (Fausch et al., 2009). Likewise, GBCT reintroductions in Colorado often occur at isolated higher elevations because they are protected from invasion by non-native species (Harig, Fausch, & Young, 2000; Young et al., 2002). These reintroduction sites coincide with streams expected to experience change in habitat characteristics due to flow reductions. Paradoxically, some of the highest-elevation study streams are limited by a cool and short summer growing season and warming climate could benefit these populations (Coleman & Fausch, 2007), especially if warming is accelerated by reduced summer flows. Conservation success of GBCT populations in Colorado in a changing climate could likely depend on the relative strengths of counteractive effects of warming temperature and reduced flows. Given the spatially heterogeneous effects of physical habitat change and uncertainties related to climate change projections, this study suggests that a GBCT conservation approach that establishes and protects populations along elevational and geomorphological gradients could build a portfolio that buffers against future uncertainties.

4.2 | Study limitations

The reliability of the results in this study are influenced by hydrologic and hydraulic uncertainties. The high elevation streamflow reductions that were used in this work are influenced by limitations in the VIC model's meteorological forcing data that are extrapolated from stations located at lower elevations. In addition, only 2 years of hydrologic field data were collected at each study site, constraining the conditions used for model calibrations and future flow projections. In addition, VIC model results fail to account for the heterogeneity in

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

streamflow recession rates or snowmelt rates (Mote, Li, Lettenmaier, Xiao, & Engel, 2018; Wenger et al., 2010), especially at high elevations. All these limitations highlight the benefits of more robust streamflow gauging in headwater streams.

To provide historical context to the measured M30MD, in 2019 and 2020, precipitation in Colorado averaged 480.3 and 310.6 mm (NCEI, 2023), compared to a historic average of 460.2 mm for the years 1977 to 2006. Because the simulated M30MD discharge values are likely lower than historic values obtained from the Western US Streamflow Metrics database, estimated future habitat characteristics for the years 2040 and 2080 may result in slightly overpredicted changes in magnitude of velocity, depth, and wetted perimeter.

5 | CONCLUSION

This study demonstrates changes in GBCT habitat caused by climate change forcing of streamflow reductions across the Southern Rocky Mountains. A unique component of this study was the combination of field collection and modelling predictions of GBCT habitat characteristics over a range of sites throughout Colorado. Results from this large distribution of study sties suggest that mean summer flow changes could result in the largest relative reduction of GBCT habitat at sites characterized by high elevations, steep slopes, and large substrate. Sites with these characteristics are used for GBCT reintroduction efforts (Young et al., 2002), thus highlighting the importance of establishing conservation measures along elevational and geomorphological gradients to buffer against future uncertainties and create GBCT population resilience.

ACKNOWLEDGMENTS

We thank Marissa Karpack for her assistance in collecting field data. This work was supported by funding from the US Geological Survey. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are availabile in a Science Base Data Release: https://doi.org/10.5066/P9WNCINC.

ORCID

Chenchen Ma https://orcid.org/0000-0001-5437-2895
Ryan R. Morrison https://orcid.org/0000-0002-8612-1684
Daniel C. White https://orcid.org/0000-0001-8376-8469
James Roberts https://orcid.org/0000-0002-4193-610X
Yoichiro Kanno https://orcid.org/0000-0001-8452-5100

REFERENCES

Benejam, L., Angermeier, P. L., Munné, A., & García-Berthou, E. (2010). Assessing effects of water abstraction on fish assemblages in Mediterranean streams. *Freshwater Biology*, *55*(3), 628–642. https://doi.org/10.1111/j.1365-2427.2009.02299.x

Beniston, M. (2003). Climatic change in mountain regions: A review of possible impacts. In H. F. Diaz (Ed.), *Climate variability and change in high elevation regions: Past, present & future* (pp. 5–31). Springer Netherlands. https://doi.org/10.1007/978-94-015-1252-7_2

Berghuijs, W. R., Woods, R. A., & Hrachowitz, M. (2014). A precipitation shift from snow towards rain leads to a decrease in streamflow. *Nature Climate Change*, *4*(7), 583–586. https://doi.org/10.1038/nclimate2246

Bjornn, J. R., & Reiser, D. W. (1991). Habitat requirements of salmonids in streams. In W. R. Meehan (Ed.), *Influence of Forest and rangeland management on salmonids fishes and habitats* (pp. 83–138). American Fisheries Society.

Bradford, M. J., & Heinonen, J. S. (2008). Low flows, instream flow needs and fish ecology in small streams. *Canadian Water Resources Journal*, *33*(2), 165–180. https://doi.org/10.4296/cwrj3302165

Chow, V. T. (1959). *Open-Channel hydraulics*. McGraw Hill.

Clow, D. W. (2010). Changes in the timing of snowmelt and streamflow in Colorado: A response to recent warming. *Journal of Climate*, *23*(9), 2293–2306. https://doi.org/10.1175/2009JCLI2951.1

Coleman, M. A., & Fausch, K. D. (2007). Cold summer temperature limits recruitment of Age-0 cutthroat trout in high-elevation Colorado streams. *Transactions of the American Fisheries Society*, *136*(5), 1231–1244. https://doi.org/10.1577/T05-244.1

Colvin, S. A. R., Sullivan, S. M. P., Shirey, P. D., Colvin, R. W., Winemiller, K. O., Hughes, R. M., Fausch, K. D., Infante, D. M., Olden, J. D., Bestgen, K. R., Danehy, R. J., & Eby, L. (2019). Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries*, *44*(2), 73–91. https://doi.org/10.1002/fsh.10229

Cook, N., Rahel, F. J., & Hubert, W. A. (2010). Persistence of Colorado River cutthroat trout populations in isolated headwater streams of Wyoming. *Transactions of the American Fisheries Society*, *139*(5), 1500–1510. https://doi.org/10.1577/T09-133.1

Coon, W. F. (1998). *Estimation of roughness coefficients for natural stream channels with vegetated banks*. U.S. Geological Survey.

Ducharne, A. (2008). Importance of stream temperature to climate change impact on water quality. *Hydrology and Earth System Sciences*, *12*(3), 797–810. https://doi.org/10.5194/hess-12-797-2008

Fausch, K. D., Rieman, B. E., Dunham, J. B., Young, M. K., & Peterson, D. P. (2009). Invasion vs. isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology*, *23*(4), 859–870. https://doi.org/10.1111/j.1523-1739.2008.01159.x

Ferguson, R. (2007). Flow resistance equations for gravel- and boulder-bed streams. *Water Resources Research*, *43*(5), W05427. https://doi.org/10.1029/2006WR005422

Furey, P. R., Kampf, S. K., Lanini, J. S., & Dozier, A. Q. (2012). A stochastic conceptual modeling approach for examining the effects of climate change on Streamflows in mountain basins. *Journal of Hydrometeorology*, *13*(3), 837–855. https://doi.org/10.1175/JHM-D-11-037.1

Garbe, J., Beevers, L., & Pender, G. (2016). The interaction of low flow conditions and spawning brown trout (Salmo trutta) habitat availability. *Ecological Engineering*, *88*, 53–63. https://doi.org/10.1016/j.ecoleng.2015.12.011

Guyette, R. P., & Rabeni, C. F. (1995). Climate response among growth increments of fish and trees. *Oecologia*, *104*(3), 272–279. https://doi.org/10.1007/BF00328361

Hakala, J. P., & Hartman, K. J. (2004). Drought effect on stream morphology and brook trout (Salvelinus fontinalis) populations in forested headwater streams. *Hydrobiologia*, *515*(1), 203–213. https://doi.org/10.1023/B:HYDR.0000027330.12182.24

Hammond, J. C., & Kampf, S. K. (2020). Subannual streamflow responses to rainfall and snowmelt inputs in snow-dominated watersheds of the Western United States. *Water Resources Research*, *56*(4), e2019WR026132. https://doi.org/10.1029/2019WR026132

Harig, A. L., & Fausch, K. D. (2002). Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological*

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Applications, *12*(2), 535–551. https://doi.org/10.1890/1051-0761(2002)012[0535:MHRFET]2.0.CO;2

Harig, A. L., Fausch, K. D., & Young, M. K. (2000). Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management*, *20*(4), 994–1004. https://doi.org/10.1577/1548-8675(2000)020<0994:FISOGC>2.0.CO;2

Harpold, A., Brooks, P., Rajagopal, S., Heidbuchel, I., Jardine, A., & Stielstra, C. (2012). Changes in snowpack accumulation and ablation in the intermountain west. *Water Resources Research*, *48*(11), W11501. https://doi.org/10.1029/2012WR011949

Harvey, B. C., Nakamoto, R. J., & White, J. L. (2006). Reduced streamflow lowers dry-season growth of rainbow trout in a small stream. *Transactions of the American Fisheries Society*, *135*(4), 998–1005. https://doi.org/10.1577/T05-233.1

Harvey, B. C., & Stewart, A. J. (1991). Fish size and habitat depth relationships in headwater streams. *Oecologia*, *87*(3), 336–342. https://doi.org/10.1007/BF00634588

Heggenes, J., & Borgstrom, R. (1988). Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in three small streams. *Journal of Fish Biology*, *33*(6), 885–894. https://doi.org/10.1111/j.1095-8649.1988.tb05536.x

Heggenes, J., Northcote, T. G., & Peter, A. (1991). Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(8), 1364–1370. https://doi.org/10.1139/f91-163

Huntsman, B. M., Lynch, A. J., & Caldwell, C. A. (2021). Interacting effects of density-dependent and density-independent factors on growth rates in southwestern cutthroat trout populations. *Transactions of the American Fisheries Society*, *150*(5), 651–664. https://doi.org/10.1002/tafs.10319

Jarrett, R. (1992). Hydraulics of mountain Rivers. In B. C. Yen (Ed.), *Channel flow resistance: Centennial of Manning's formula* (p. 460). Water Resources Publication.

Jefferson, A. J. (2011). Seasonal vs. transient snow and the elevation dependence of climate sensitivity in maritime mountainous regions. *Geophysical Research Letters*, *38*(16), L16402. https://doi.org/10.1029/2011GL048346

Jolliffe, I. T. (2002). *Principal component analysis* (2nd ed.). Springer.

Jolliffe, I. T., & Cadima, J. (2016). Principal component analysis: A review and recent developments. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *374*(2065), 20150202. https://doi.org/10.1098/rsta.2015.0202

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Klos, P. Z., Link, T. E., & Abatzoglou, J. T. (2014). Extent of the rain-snow transition zone in the western U.S. under historic and projected climate. *Geophysical Research Letters*, *41*(13), 4560–4568. https://doi.org/10.1002/2014GL060500

Kovach, R. P., Muhlfeld, C. C., Al-Chokhachy, R., Dunham, J. B., Letcher, B. H., & Kershner, J. L. (2016). Impacts of climatic variation on trout: A global synthesis and path forward. *Reviews in Fish Biology and Fisheries*, *26*(2), 135–151. https://doi.org/10.1007/s11160-015-9414-x

Leppi, J. C., DeLuca, T. H., Harrar, S. W., & Running, S. W. (2012). Impacts of climate change on august stream discharge in the central-Rocky Mountains. *Climatic Change*, *112*(3–4), 997–1014. https://doi.org/10.1007/s10584-011-0235-1

Liu, Y. B., Gebremeskel, S., De Smedt, F., Hoffmann, L., & Pfister, L. (2004). Simulation of flood reduction by natural river rehabilitation using a distributed hydrological model. *Hydrology and Earth System Sciences Discussions*, *8*(6), 1129–1140.

Mantua, N., Tohver, I., & Hamlet, A. (2010). Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington state. *Climatic Change*, *102*(1–2), 187–223. https://doi.org/10.1007/s10584-010-9845-2

May, C. L., & Lee, D. C. (2004). The relationships among In-Channel sediment storage, Pool depth, and summer survival of juvenile salmonids in Oregon coast range streams. *North American Journal of Fisheries Management*, *24*(3), 761–774. https://doi.org/10.1577/M03-073.1

Meier, W. K., & Reichert, P. (2005). Mountain streams—Modeling hydraulics and substance transport. *Journal of Environmental Engineering*, *131*(2), 252–261. https://doi.org/10.1061/(ASCE)0733-9372(2005)131:2(252)

Metcalf, J. L., Love Stowell, S., Kennedy, C. M., Rogers, K. B., McDonald, D., Epp, J., Keepers, K., Cooper, A., Austin, J. J., & Martin, A. P. (2012). Historical stocking data and 19th century DNA reveal human-induced changes to native diversity and distribution of cutthroat trout. *Molecular Ecology*, *21*(21), 5194–5207. https://doi.org/10.1111/mec.12028

Meyer, J. L., Strayer, D. L., Wallace, J. B., Eggert, S. L., Helfman, G. S., & Leonard, N. E. (2007). The contribution of headwater streams to biodiversity in river networks. *JAWRA Journal of the American Water Resources Association*, *43*(1), 86–103. https://doi.org/10.1111/j.1752-1688.2007.00008.x

Milly, P. C. D., & Dunne, K. A. (2020). Colorado River flow dwindles as warming-driven loss of reflective snow energizes evaporation. *Science*, *367*(6483), 1252–1255. https://doi.org/10.1126/science.aay9187

Montgomery, D. R., & Buffington, J. M. (1997). Channel-reach morphology in mountain drainage basins. *GSA Bulletin*, *109*(5), 596–611. https://doi.org/10.1130/0016-7606(1997)109<0596:CRMIMD>2.3.CO;2

Morita, K., Sahashi, G., & Tsuboi, J. (2016). Altitudinal niche partitioning between white-spotted charr (*Salvelinus leucomaenis*) and masu salmon (*Oncorhynchus masou*) in a Japanese river. *Hydrobiologia*, *783*(1), 93–103. https://doi.org/10.1007/s10750-015-2571-z

Mote, P. W., Li, S., Lettenmaier, D. P., Xiao, M., & Engel, R. (2018). Dramatic declines in snowpack in the western US. *Npj Climate and Atmospheric Science*, *1*(1), 2. https://doi.org/10.1038/s41612-018-0012-1

Nakano, S., Kitano, S., Nakai, K., & Fausch, K. D. (1998). Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environmental Biology of Fishes*, *52*(1–3), 345–355. https://doi.org/10.1023/A:1007359826470

NCEI. (2023). NOAA National Centers for Environmental Information, Climate at a Glance: Statewide Time Series. https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/statewide/time-series

Nislow, K. H., Folt, C. L., & Parrish, D. L. (1999). Favorable foraging locations for young Atlantic salmon: Application to habitat and population restoration. *Ecological Applications*, *9*(3), 1085–1099. https://doi.org/10.1890/1051-0761(1999)009[1085:FFLFYA]2.0.CO;2

Owens, H. W., & Keeley, E. R. (2022). Quantifying the foodscape for stream-dwelling cutthroat trout reveals spatial and temporal ranges of resource exploitation and energy intake. *Transactions of the American Fisheries Society*, *151*(4), 441–452. https://doi.org/10.1002/tafs.10360

Papadaki, C., Soulis, K., Muñoz-Mas, R., Martinez-Capel, F., Zogaris, S., Ntoanidis, L., & Dimitriou, E. (2016). Potential impacts of climate change on flow regime and fish habitat in mountain rivers of the South-Western Balkans. *Science of the Total Environment*, *540*, 418–428. https://doi.org/10.1016/j.scitotenv.2015.06.134

Pederson, G. T., Betancourt, J. L., & McCabe, G. J. (2013). Regional patterns and proximal causes of the recent snowpack decline in the Rocky Mountains, U.S. *Geophysical Research Letters*, *40*(9), 1811–1816. https://doi.org/10.1002/grl.50424

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Penaluna, B. E., Dunham, J. B., & Andersen, H. V. (2021). Nowhere to hide: The importance of instream cover for stream-living coastal cutthroat trout during seasonal low flow. *Ecology of Freshwater Fish*, *30*(2), 256–269. https://doi.org/10.1111/eff.12581

Piccolo, J. J., Hughes, N. F., & Bryant, M. D. (2008). Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(2), 266–275. https://doi.org/10.1139/f07-172

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Reid, D. E., & Hickin, E. J. (2008). Flow resistance in steep mountain streams. *Earth Surface Processes and Landforms*, *33*(14), 2211–2240. https://doi.org/10.1002/esp.1682

Roberts, J. J., Fausch, K. D., Hooten, M. B., & Peterson, D. P. (2017). Nonnative trout invasions combined with climate change threaten persistence of isolated cutthroat trout populations in the southern Rocky Mountains. *North American Journal of Fisheries Management*, *37*(2), 314–325. https://doi.org/10.1080/02755947.2016.1264507

Roberts, J. J., Fausch, K. D., Peterson, D. P., & Hooten, M. B. (2013). Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin. *Global Change Biology*, *19*(5), 1383–1398. https://doi.org/10.1111/gcb.12136

Rood, S. B., Pan, J., Gill, K. M., Franks, C. G., Samuelson, G. M., & Shepherd, A. (2008). Declining summer flows of Rocky Mountain rivers: Changing seasonal hydrology and probable impacts on floodplain forests. *Journal of Hydrology*, *349*(3–4), 397–410. https://doi.org/10.1016/j.jhydrol.2007.11.012

Rosenfeld, J. S., & Boss, S. (2001). Fitness consequences of habitat use for juvenile cutthroat trout: Energetic costs and benefits in pools and riffles. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(3), 585–593. https://doi.org/10.1139/f01-019

Rumsey, C. A., Miller, M. P., Susong, D. D., Tillman, F. D., & Anning, D. W. (2015). Regional scale estimates of baseflow and factors influencing baseflow in the upper Colorado River basin. *Journal of Hydrology: Regional Studies*, *4*, 91–107. https://doi.org/10.1016/j.ejrh.2015.04.008

Scalzitti, J., Strong, C., & Kochanski, A. K. (2016). A 26 year high-resolution dynamical downscaling over the Wasatch Mountains: Synoptic effects on winter precipitation performance. *Journal of Geophysical Research-Atmospheres*, *121*(7), 3224–3240. https://doi.org/10.1002/2015JD024497

Schlosser, I. J. (1995). Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia*, *303*(1), 71–81. https://doi.org/10.1007/BF00034045

Somers, L. D., & McKenzie, J. M. (2020). A review of groundwater in high mountain environments. *WIREs Water*, *7*(6), e1475. https://doi.org/10.1002/wat2.1475

Sotiropoulos, J. C., Nislow, K. H., & Ross, M. R. (2006). Brook trout, Salvelinus fontinalis, microhabitat selection and diet under low summer stream flows. *Fisheries Management and Ecology*, *13*(3), 149–155. https://doi.org/10.1111/j.1365-2400.2006.00487.x

Tague, C., & Dugger, A. L. (2010). Ecohydrology and climate change in the mountains of the Western USA – A review of research and opportunities. *Geography Compass*, *4*(11), 1648–1663. https://doi.org/10.1111/j.1749-8198.2010.00400.x

US Army Corps of Engineers. (2016). HEC-RAS River Analysis System User's Manual. US Army Corps of Engineers Hydrologic Engineering Center.

Uthe, P., Al-Chokhachy, R., Shepard, B. B., Zale, A. V., & Kershner, J. L. (2019). Effects of climate-related stream factors on patterns of individual summer growth of cutthroat trout. *Transactions of the American Fisheries Society*, *148*(1), 21–34. https://doi.org/10.1002/tafs.10106

van Vliet, M. T. H., Yearsley, J. R., Franssen, W. H. P., Ludwig, F., Haddeland, I., Lettenmaier, D. P., & Kabat, P. (2012). Coupled daily streamflow and water temperature modelling in large river basins. *Hydrology and Earth System Sciences*, *16*(11), 4303–4321. https://doi.org/10.5194/hess-16-4303-2012

VerWey, B. J., Kaylor, M. J., Garcia, T. S., & Warren, D. R. (2018). Effects of a severe drought on summer abundance, growth, and movement of cutthroat trout In a Western Oregon headwater stream. *Northwestern Naturalist*, *99*(3), 209–221. https://doi.org/10.1898/NWN17-27.1

Vezza, P., Parasiewicz, P., Spairani, M., & Comoglio, C. (2014). Habitat modeling in high-gradient streams: The mesoscale approach and application. *Ecological Applications*, *24*(4), 844–861. https://doi.org/10.1890/11-2066.1

Vøllestad, L. A., & Olsen, E. M. (2008). Non-additive effects of density-dependent and density-independent factors on brown trout vital rates. *Oikos*, *117*(11), 1752–1760. https://doi.org/10.1111/j.1600-0706.2008.16872.x

Watts, A., Grant, G., & Safeeq, M. (2016). *Flows of the future—How will climate change affect streamflows in the Pacific Northwest?* (Science Findings 187.; p. 5). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. http://www.fs.usda.gov/treesearch/pubs/52180

Wenger, S. J., Luce, C. H., Hamlet, A. F., Isaak, D. J., & Neville, H. M. (2010). Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resources Research*, *46*(9), W09513. https://doi.org/10.1029/2009WR008839

White, D. C., Morrison, R. R., & Wohl, E. (2022). Fire and ice: Winter flooding in a southern Rocky Mountain stream after a wildfire. *Geomorphology*, *413*, 108370. https://doi.org/10.1016/j.geomorph.2022.108370

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (2nd ed.). Springer International Publishing: Imprint: Springer. https://doi.org/10.1007/978-3-319-24277-4

Williams, J. E., Haak, A. L., Neville, H. M., & Colyer, W. T. (2009). Potential consequences of climate change to persistence of cutthroat trout populations. *North American Journal of Fisheries Management*, *29*(3), 533–548. https://doi.org/10.1577/M08-072.1

Wipfli, M. S., & Baxter, C. V. (2010). Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. *Fisheries*, *35*(8), 373–387. https://doi.org/10.1577/1548-8446-35.8.373

Wohl, E. (2010). *Mountain Rivers revisited*. American Geophysical Union.

Wohl, E. (2017). The significance of small streams. *Frontiers of Earth Science*, *11*(3), 447–456. https://doi.org/10.1007/s11707-017-0647-y

Wohl, E. E. (2001). *Virtual Rivers: Lessons from the mountain Rivers of the Colorado front range*. Yale University Press.

Wolman, M. G. (1954). A method of sampling coarse river-bed material. *Eos, Transactions American Geophysical Union*, *35*(6), 951–956. https://doi.org/10.1029/TR035i006p00951

Xu, C. L., Letcher, B. H., & Nislow, K. H. (2010). Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: Effects of water temperature and stream flow. *Journal of Fish Biology*, *76*(10), 2342–2369. https://doi.org/10.1111/j.1095-8649.2010.02619.x

Yochum, S. E., Bledsoe, B. P., David, G. C. L., & Wohl, E. (2012). Velocity prediction in high-gradient channels. *Journal of Hydrology*, *424–425*, 84–98. https://doi.org/10.1016/j.jhydrol.2011.12.031

Yochum, S. E., Comiti, F., Wohl, E., David, G., & Mao, L. (2014). *Photographic guidance for selecting flow resistance coefficients in high-gradient channels* (Gen. Tech. Rep. RMRS-GTR-323; p. 91). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Young, M. K., & Harig, A. L. (2001). A critique of the recovery of greenback cutthroat trout. *Conservation Biology*, *15*(6), 1575–1584. https://doi.org/10.1046/j.1523-1739.2001.00291.x

Young, M. K., Harig, A. L., Rosenlund, B., & Kennedy, C. (2002). Recovery history of greenback cutthroat trout: Population characteristics,

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

hatchery involvement, and bibliography, version 1.0 (RMRS-GTR-88; p. 25). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. http://www.fs.usda.gov/treesearch/pubs/4591

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ma, C., Morrison, R. R., White, D. C., Roberts, J., & Kanno, Y. (2023). Climate change impacts on native cutthroat trout habitat in Colorado streams. *River Research and Applications*, *39*(5), 970–986. https://doi.org/10.1002/rra.4122

15351467, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/rra.4122 by Cochrane Japan, Wiley Online Library on [02/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License