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ARTICLE

Freshwater Ecology

Contrasting apex predator responses to experimentally reduced flow and increased temperature in a headwater stream

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Abstract

Changing climate conditions are expected to cause increases in the frequency and severity of drought conditions in many areas around the world, including the Pacific Northwest region of North America. While drought impacts manifest across the landscape, headwater streams are particularly susceptible to droughts due to limited deep-water habitats and low water volumes that allow for substantial increases in water temperature. While low volumes of water and increased stream temperature will likely affect all aquatic species to some degree, the response of different taxa to these impacts is expected to vary with differences in physiological needs and habitat preferences among species. Using a before–after control-impact (BACI) experimental design, this study investigates how reduced streamflow and increased stream temperature affect the two dominant apex predators in headwater streams of the Pacific Northwest, coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and coastal giant salamander (*Dicamptodon tenebrosus*). In a second-order stream in the H.J. Andrews Experimental Forest in OR, USA, experimental flow diversions created decoupled drought conditions of reduced streamflow and elevated temperatures. Low-flow conditions were created by diverting water around a 100-m stream reach and this diverted water was passively warmed before re-entering a downstream channel to create an increased temperature reach. We compared fish and salamander abundances and stream habitat in an upstream unmanipulated reference reach to the two experimental reaches. Relative increases in temperature ranged between 0.41 and 0.63°C, reflecting realistic stream warming in this region during drought events. Trout responded positively to increased temperatures, showing an increase in abundance, biomass, condition factor, and growth, whereas salamanders responded negatively in all metrics except condition. The low-flow reach diverted approximately 50% of the flow, resulting in a relative pool area reduction of about 20%. Relative to the reference reach, salamanders displayed a net positive abundance response while trout declined in the low-flow reach. The contrasting responses of these populations to decoupled drought conditions suggest that interactions of flow and temperature changes together will influence drought responses of the vertebrate communities of headwater streams.

KEYWORDS
BACI, climate change, drought, freshwater populations, salamanders, trout

INTRODUCTION

Changing climate and decreasing snowpack in mountainous landscapes across the western United States are expected to contribute to more frequent and severe drought in many areas across this region (Mantua et al., 2010; Mote et al., 2018; Verfaillie et al., 2018). Drought conditions not only result in decreased flows but also include warmer temperatures particularly relevant in western systems with long dry summers. Headwater streams, which constitute 60%–80% of the stream length in a watershed (Shreve, 1969), may be buffered to some degree by groundwater controls (Kaule & Gilfedder, 2021; Segura et al., 2019), but overall they are ecosystems vulnerable to drought because deep-water habitats are limited, and low water volumes enhance susceptibility to temperature increases. Cold-water adapted biota, which are often found in headwater environments, can be especially sensitive to these flow reductions and temperature increases (Bennett et al., 2012; Isaak et al., 2012). While an increase in the frequency and severity of drought conditions experienced in streams can have broad impacts across all aquatic species, the individual drought components of increased stream temperature and reduced stream flow may have different effects among species due to differences in physiological needs and habitat preferences. Understanding how decoupled drought conditions—specifically reduced flow and increased stream temperature—impact sympatric populations of trout and salamanders may provide insights into the mechanisms driving potential shifts in stream communities.

Reduced streamflow and increased stream temperature can have adverse effects on salmonids (Arismendi et al., 2013, 2024; Kaylor et al., 2019; VerWey et al., 2018). Salmonids often rely on deepwater habitats (defined in many headwater systems as greater than 25 cm (Kaylor et al., 2019)) in headwater streams (Berg et al., 1998; Kennedy & Strange, 1982); therefore, drought-driven reductions in discharge can negatively impact fish populations. For instance, age 1+ and older brook trout (*Salvelinus fontinalis*) populations declined in Montana, USA, when 90% of the flow was diverted, although the influence on the number of young-of-year (YOY) was inconsistent (Kraft, 1972). Additionally, in an experiment in northern California, USA, fish grew about 8.5 times less in a reach with reduced streamflow relative to an unmanipulated reference (Harvey et al., 2006). In contrast, increases in stream discharge have been found to promote growth rates in resident cutthroat trout (*Oncorhynchus clarkii bouvieri*) due to higher drifting prey availability and greater habitat availability (Uthe et al., 2019). Reductions in flow clearly affect the abundance and growth of salmonids; however, during a drought fish in headwater streams generally experience both decreased flow and increased temperatures (Kaylor et al., 2019).

Increased temperatures that often accompany flow reductions in drought conditions can also negatively impact stream salmonids. For example, temperature increases and reduced flows via a water diversion have been found to result in a significant reduction in brook trout (*S. fontinalis*) growth (Nuhfer et al., 2017). More broadly, across the western United States, increases in temperature are widely seen as one of the greatest climate change threats for stream salmonids (Isaak et al., 2012; Wenger et al., 2011). These studies collectively demonstrate that changing flow and increasing water temperature can impact fish abundance and growth. However, most drought studies focus on a singular factor of drought or evaluate the drought event with coupled temperature and flow changes, making it difficult to disentangle the relative influences of reduced flow or increased stream temperature on salmonid populations.

Evaluation of stream salamander responses to drought has been more variable. In western Oregon, coastal giant salamander (*Dicamptodon tenebrosus*) condition factor declined significantly across multiple headwater streams in response to a severe drought, but abundance was not consistently impacted (Kaylor et al., 2019). Across streams in the central Appalachian Mountains, plethodontid salamanders declined substantially in condition and abundance in response to drought, which was attributed to decreasing prey availability and increased competition for both food and habitat (Currinder et al., 2014). However, adult dusky salamander occupancy across 17 headwater streams during a drought in the same region was found to be largely unimpacted, but juvenile occupancy in that study did decline (Price et al., 2012). The authors attributed reduced juvenile occupancy to multiple potential factors including mortality, reductions in oviposition in the streams, and increased use of hyporheic habitat by juveniles thereby decreasing capture probability. The use of hyporheic habitat by pacific salamanders is suggested as a key factor providing insulation from seasonal drought (Feral et al., 2005) and may be hypothesized to yield similar resistance to larger and more severe events. As shown, salamander responses to drought are quite varied, highlighting the need for a deeper understanding of how decoupled drought effects and other apex predator communities may influence and interact with salamander populations.

Varying drought conditions will affect species differently depending upon the physiology and behavior of the organisms and the underlying conditions of the system experiencing the drought. For example, in Oregon, trout and salamanders were both negatively impacted by a severe drought in 2015, but the nature of the impact differed (Kaylor et al., 2019). While trout abundances declined across nine headwater streams relative to previous years, salamander abundances did not change substantially. In contrast to abundance, trout condition factor remained comparable while salamander condition factor declined consistently across all sites (Kaylor et al., 2019). Considering species interactions in particular, a study of fish responses to drought across a series of prairie streams in the midwestern United States found that when drought conditions isolated fish in pools, the interaction of pool conditions with physiological constraints of different fish species determined which taxa were extirpated from a given pool (Hopper et al., 2020). These studies illustrate various pathways through which drought may impact headwater stream vertebrates, suggesting the potential for different "winners" and "losers" depending on the specific habitat changes associated with each drought condition.

We can conduct empirical studies to evaluate drought impacts on aquatic biota during an event, but the simultaneous changes in flow and temperature make it difficult to separate the effects of each factor on biota. In this study, we established an experiment to evaluate how the two dominant aquatic apex predators in headwater streams in the western United States (trout and salamanders) respond to each of the two isolated dominant components of a drought (reductions in flow and increases in water temperature) at a reach scale. Our goal was to gain insight into which factors most strongly affect which taxa to increase our understanding of how headwater apex predator communities may change in different stream systems in a future with increasing drought frequency and severity. We hypothesized that a reduction in flow will decrease trout and salamander abundance due to a decrease in physical habitat (leading to greater inter- and intra-specific interactions). Given the cooler initial temperatures in our focal system, we hypothesized that temperature increases would improve stream productivity, ultimately increasing species growth and condition factor. However, we were also testing the alternative hypothesis based on bioenergetics models that even moderate increases in temperatures could be stressful for fish due to increased metabolic demand (Beakes et al., 2014). Given the competitive pressures from the presence of both species in these small systems, we expected this experiment to reveal distinct "winners" and "losers," associated with these drought factors driving the state change.

METHODS

Study site

The H.J. Andrews Experimental Forest (HJA) is a long-term ecological research site that lies within the Oregon Cascade Mountain Range and encompasses a total of 6400 ha of forested hillslopes. At lower elevations, the forest consists primarily of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), whereas at higher elevations, the Pacific silver fir (*Abies amabilis*) dominates. The riparian areas of the headwater streams are characterized by vine maple (*Acer circinatum*), red alder (*Alnus rubra*), and western rhododendron (*Rhododendron macrophyllum*). The HJA is dominated by late succession forest but includes patches of 40–70-year-old plantations that collectively occur across 25% of the watershed. This region receives on average 2330 mm of precipitation annually (PRISM Climate Group, 2014) and has a Mediterranean climate with long dry summer periods of low-flow conditions.

During the summer of 2022, three study reaches were established along a second-order western tributary of McRae Creek, known as McRae Creek Tributary-West (hereafter "MCTW"). This tributary is situated in the upper headwaters of the larger HJA basin (Figure 1). Mean stream bankfull width in the three reaches was 3.1 m (Table 1). A small (fishless and seasonally intermittent) tributary enters MCTW between the upstream site and the two downstream sites (Figure 2). Stream substrates in all three reaches are dominated by boulder and cobble sizes. Additionally, two stream vertebrate species, coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and

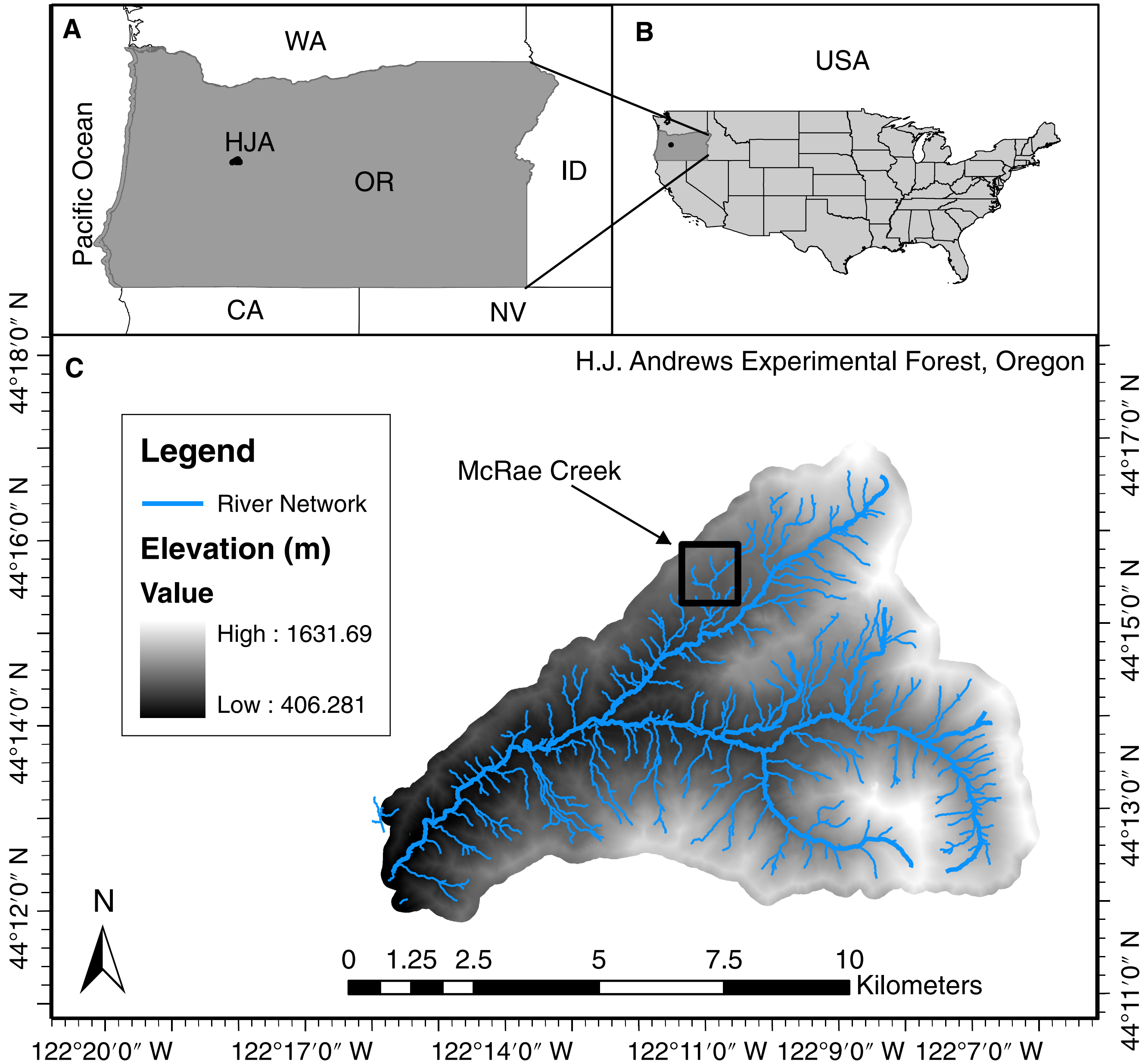

FIGURE 1 H.J. Andrews Experimental Forest (HJA) location in Oregon, USA, and the McRae Creek Tributary West (MCTW) study site within the Lookout Creek stream network. Lighter black scale indicates higher elevation (in meters).

coastal giant salamanders (*D. tenebrosus*), are present in all three reaches.

Study design

To examine the relative impact of decoupled drought conditions of reduced flow and increased water temperature, we established three open-system study reaches: (1) an upstream reference reach that was unaltered, (2) a middle reach in which flow was decreased (diverted) to mimic low-flow drought conditions, and (3) a downstream warmed reach in which diverted streamflow was passively warmed in a coil system and reintroduced downstream to elevate stream temperatures and mimic drought temperature conditions (Figure 2). Henceforth, we will refer to the upstream reference reach as the "Reference reach," we will refer to the reach with the decreased flow as the "Low-flow reach," and we will refer to the reach with elevated water temperature as the "Warmed reach."

To create these conditions in a remote landscape, we developed a passive (gravity-fed) flow diversion system (Figure 2B). The Low-flow reach was created by placing a temporary plywood barrier across the stream in which there were two 10 cm holes. A 10 cm line (flexible plastic

TABLE 1 Pre-treatment and post-treatment characteristics (mean bankfull width, mean wetted width, reach length, reach area, total pool area, and mean residual pool depth) of the Reference, Low-flow, and Warmed reaches, and the percent change (percent change in reach area and percent change in pool area) between the pre- and post-treatment surveys.

Site	Date	Mean bankfull width (m)	Mean wetted width (m)	Reach length (m)	Reach area (m^2)	% change in reach area	Total pool area (m^2)	% change in pool area	Mean residual pool depth (cm)
Pre-treatment									
Reference	Jul 22, 2022	3.10	1.83	45	82.4	…	14.4	…	26.8
Low-flow	Jul 19, 2022	3.12	2.25	50	112.3	…	29.0	…	18.4
Warmed	Jul 19, 2022	3.13	1.92	45	86.4	…	17.6	…	15.2
Post-treatment									
Reference	Sep 08, 2022	3.10	1.54	45	69.3	−15.8	13.9	−3.6	26.3
Low-flow	Sep 09, 2022	3.12	1.59	50	79.3	−29.4	19.9	−31.4	19.6
Warmed	Sep 09, 2022	3.13	1.47	45	65.9	−23.7	15.7	−11.1	13.7

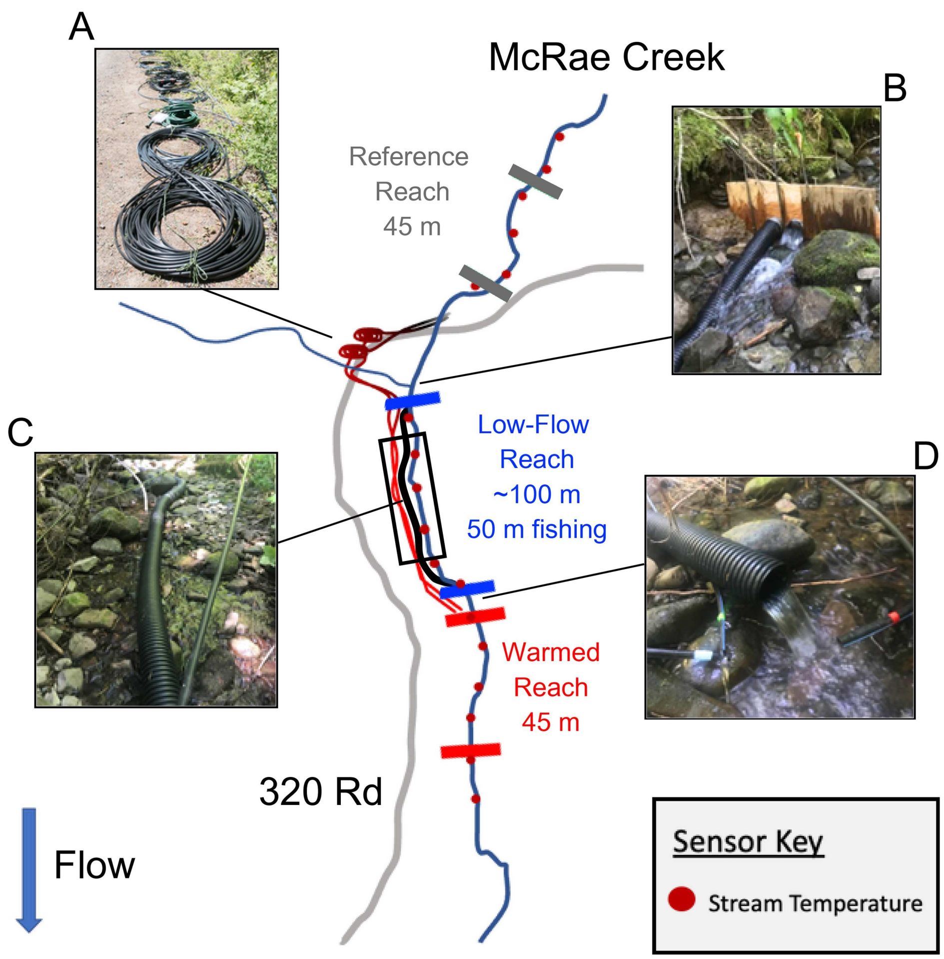

FIGURE 2 General layout of the experimental design in McRae Creek Tributary West (MCTW). (A) Multiple 1.2 cm line coil system that siphons water from an upstream location, passively warms the water through sun exposure, and re-enters below the Low-flow reach. (B) Flow diversion system situated upstream of the Low-flow reach, diverting approximately 50% of the stream flow through a 10 cm line while allowing the remaining 50% to flow continuously through the stream. (C) The 10 cm line carrying water from the flow diversion system, reentering below the Low-flow reach. (D) Location where the 10 cm line and the 1.2 cm lines with warmed water re-enter the stream just above the Warmed reach. Photo credit: Dana Warren.

pipe) was selected to accommodate the transport of even the largest fish typically found in a stream of this size. We placed the 10 cm line through one hole ("diversion line") and left one hole empty to allow flow and fish to pass through the barrier ("pass-through line"). This was intended to allow approximately half of the flow to remain in the channel (Figure 2B). The goal was not to fully dewater the channel, but instead to reduce discharge proportionally to flow in the stream. The pass-through line was positioned low enough within the flow diversion barrier to ensure potential fish passage. The diversion line was approximately 100 m in length and redirected approximately 50% of the streamflow (Figure 2C). The diverted water in this diversion line was reintroduced to the channel 100 m downstream from the plywood barrier and 30 m downstream of the lower end of the focal Low-flow study reach. The outflow from this flow diversion line re-entered the stream 8 m upstream of the start of the Warmed reach (Figure 2D).

The Warmed reach was created by heating water passively in coiled tubing (Figure 2A). In addition to the main 10 cm diversion line (which also heated the water slightly relative to the stream), eight 1.2 cm diversion lines siphoned water from an upstream pool (above the Low-flow reach but below the Reference reach) and heated the water for the Warmed reach. The flow in these lines also contributed to flow diversion but was a small portion of volume relative to the 10 cm diversion line. The 1.2 cm warming lines were arranged in coils that were exposed to direct sunlight during the day by placing them along the side of the USFS 320 Rd. that runs parallel to the study reaches (Figure 2A). The warmed water in the coiled 1.2 cm lines was reintroduced to the stream approximately 8 m above the upstream end of the Warmed reach in an area where there was a high degree of mixing, so the warmed water could be fully incorporated into the flow.

Our focal fish surveys in the Reference and Warmed reaches were 45 m long, while fish surveys in the Low-flow reach were conducted over 50 m. The full extent of area with reduced flow was approximately 100 m, but to avoid potential edge effects near the start and end of that treatment, we focused on the central area of the Low-flow section for electrofishing and habitat surveys. The Low-flow survey reach began 20 m downstream of the main flow diversion and extended for 50 m. The Warmed reach began 8 m below the area of main flow reintroduction and extended downstream for 45 m.

Field methods

We deployed HOBO TidbiT v2 data loggers to measure stream temperature at the downstream end of each stream section. Loggers were deployed in July just before the launch of the reduced flow and increased temperature treatments. Although there was little to no pre-treatment data for these metrics, the loggers were left in place for three weeks after the treatments ceased to provide data on inherent temperature differences between sites. Additional temperature data loggers were placed to evaluate temperature changes across the reaches.

We quantified stream habitat in each reach, once before the treatments started (mid-July) and once during the end of the treatment period (early September) (Table 1). In each study reach, we identified and measured pool dimensions (width, length, and residual depth). Stream wetted widths were measured at cross-sections every 5 m along each reach immediately after each of the two electrofishing surveys was conducted. At every other cross-section (every ~10 m), we also collected 5–7 evenly spaced stream depth measurements and a stream bankfull width measurement.

We conducted the pre-treatment electrofishing surveys in all reaches (Reference, Low-flow, and Warmed) between July 18, 2022 and July 22, 2022. In each reach, we set block nets at the upstream and downstream ends to close the system, conducted three passes through each reach, and collected all trout (the only fish species present) and all salamanders that we found in each pass. Trout and smaller salamanders were held in aerated coolers next to each stream. Large salamanders were held separately to avoid predation during holding. All trout were anesthetized with AQUI-S, weighed (to 0.1 g), and measured (total length and fork length to nearest mm). To evaluate fish summer growth rates, every captured trout larger than 80 mm received a 9-mm Biomark PIT Tag. Visible Implant Elastomer (VIE) tags were additionally applied to all salmonids, with each reach receiving a different batch color. Salamanders were placed in a plastic bag for measurement of both vent and total length (to nearest mm) and weighed (to 0.1 g).

We returned to resurvey each study reach in early September, after approximately 7 weeks (total of 51 days) of the Low-flow and Warmed treatments. Our "post-treatment" surveys were conducted during the final days of the treatment. Only two passes were conducted on these sites due to adverse field conditions. Based on the high depletion rates that were achieved in these small headwaters in the July sampling, we are confident that two passes adequately estimated abundances in these September sampling events, particularly for trout. All fish and salamanders were fully processed (weighed and measured) following the same procedures as in the July surveys. Elastomer tag recaptures were noted, and tag numbers of recaptured PIT-tagged trout were recorded, but no new tags (elastomer or PIT) were applied in the September sampling. The flow and temperature treatments ended on September 9, 2022.

Analysis

To assess the effects of the treatments on stream temperature, we calculated the mean difference in maximum daily stream temperature between (1) the Low-flow and Reference reaches and (2) the Warmed and Reference reaches during the experiment. The loggers were removed from the streams during electrofishing, so data were not included from those days. We also calculated the total accumulated daily difference in mean temperatures for the duration of the experiment and for 21 days after the treatments ended. We compared total accumulated temperature effects of the two treatments relative to the Reference reach.

The abundance of trout and salamanders was estimated independently because they have different capture probabilities. We also separated adult trout (>1+) and YOY (0+) trout for analysis. We used multiple pass depletion to estimate abundance, and 95% CIs were determined using maximum likelihood estimation (Carle & Strub, 1978) in the Fisheries Stock Analysis package (Ogle et al., 2023) in R. Biomass of each taxa/age class was estimated as the mean mass multiplied by the abundance estimate. Error on the abundance and biomass estimates was based on capture probabilities from the depletion rate. Although 95% CI are usually symmetric boundaries around a value based on the SE of the estimate, in multiple pass depletion surveys, 95% CI are often asymmetric because they are bounded on the lower end by the total number of individuals captured (i.e., minimum of 95% CI cannot be less than the number captured). Therefore, in evaluating abundance and biomass differences between time periods within each reach, we focused our comparisons on overlap between differences of the 95% CI rather than on statistical tests based on SEs alone (per Warren & Kraft, 2003). We compared the abundance and biomass of trout and salamanders per linear meter of stream among each reach between July and September sampling events. We focus on estimates per linear meter rather than per square meter of wetted channel because the focus of this study is on whether the abundance, biomass, and condition of vertebrates within a specific section of stream changes under different conditions. Because we are changing discharge in one reach, decreases in wetted widths would affect our interpretation of how the vertebrate community in that section of stream responds to the treatment. To evaluate treatment effects in the context of the before–after control-impact (BACI) study design, we calculated the natural log of the ratio (post-treatment/pre-treatment) between the September surveys (post-treatment) and the July surveys (pre-treatment) at each of the three treatment sites. We then evaluated the response of the two treatments to that of the Reference reach.

Fulton's condition factor (Ricker 1975), a proxy estimate of fitness based on mass and length, was calculated for all trout during both sampling periods using total length, and for all salamanders during both sampling periods using vent length (center of vent). Fulton's condition factor (kc) was calculated using the following equation:

$$\mathrm{kc} = 100 \times \frac{M}{L^3}, \tag{1}$$

where M is the total mass (in grams) of the vertebrate, and L is the measured length (in centimeters) of the vertebrate, with a higher condition factor indicating greater fitness. Differences in mean condition factor between reaches were assessed using an ANOVA.

We assessed the number and condition of age 0+ trout (YOY) captured in September. Mean mass and mean condition factor of the YOY fish were compared between reaches. However, we did not make explicit comparisons between reaches in a BACI framework or make any statistical conclusions because numbers were low at all sites in September and only one YOY fish was captured across all sites in July.

We evaluated trout recaptures within a reach based on the proportion of trout marked in the July surveys that were then recaptured in the September samples for each reach using the elastomer batch marks. We assessed summer "growth" for all recaptured PIT tagged trout in each reach (although some trout lost mass). Because summer growth rates can be affected by differences in initial fish size, growth was calculated as the change in mass divided by initial mass (grams per gram). Differences in mean growth were assessed using an ANOVA.

RESULTS

Changes in habitat conditions

Stream flow declined across all sites through summer 2022 as expected given the Mediterranean climate and associated lack of summer rain in this region. Stream area declined more in the Low-flow treatment reach compared to the other two reaches, particularly regarding pool habitat. Pool area declined by 3.5% in the Reference, 11% in the Warmed, and 31% in the Low-flow during the duration of the experiment (Table 1). Responses in total area were more comparable than pool area with declines of 15% in the Reference, 24% in the Warmed, and 30% in the Low-flow (Table 1). Because reach lengths remained the same between sampling periods in each reach, these differences in total wetted area were driven by a change in stream wetted width.

Overall, during the full 51 days of the experiment, mean daily temperatures at the downstream end of the Warmed reach were an average 0.43°C warmer than the Reference reach. The mean difference in maximum daily temperatures at the upstream end of the Warmed reach was on average 0.61°C warmer than the Reference reach (Figure 3A). The downstream measurement in the Warmed reach represents the smallest potential change in the reach as temperature additions were attenuated downstream.

Water temperatures in the Low-flow reach during the experiment were also slightly elevated relative to differences during the post-treatment period (Figure 3), which we attribute to greater heating of surface waters with lower volume and therefore lower thermal mass. The mean difference in daily mean temperatures between the downstream ends of the Reference reach and the Low-flow reach during the experiment was 0.29°C, and the mean difference in maximum daily temperatures was 0.35°C. In contrast to the Warmed reach, the downstream end of the Low-flow reach represented maximum potential change as temperature increases accumulated through this reach. A logger at the upstream end of the Low-flow reach (meter 2) had a mean difference in mean daily temperatures of 0.14, only 0.03°C greater than in the after-treatment period.

Mean daily stream temperatures were slightly greater in the Low-flow and Warmed reaches relative to the upstream Reference reach during the 21 days of post-experiment temperature measurements, but daily mean differences were on average only 0.13 and 0.11°C warmer at the downstream end of the Warmed and Low-flow reaches, respectively. However, the Reference reach was warmer than the two treatment reaches on two days during the post-treatment period (Figure 3A). Maximum daily temperature differences between the downstream ends of the treatment reaches and the Reference reach during the post-experimental period were also only ~0.17°C for the Warmed and ~0.16°C for the Low-flow reaches. Mean daily temperatures in the treatment reaches were, on average, more elevated during the experiment than after the experiment (Figure 3A).

While individual mean daily temperature effects during the experiment were small, collectively, over the course of the 51-day experiment these changes amounted to a total mean degree-day increase of 22°C through the summer at the downstream end of the Warmed reach (Figure 3B), and a >25°C mean accumulated degree day increase at meter 25 of the Warmed reach. At the downstream end of the Low-flow reach, total accumulated degree day difference from the Reference reach was 14°C (Figure 3B).

Trout and salamander responses

The abundance and biomass of cutthroat trout decreased from July to September in both the Reference reach and the Low-flow reach during the experiment, with significantly lower abundances and significantly less biomass in each reach in September relative to July based on the overlap of the asymmetric 95% CI for abundance (Figure 4A) and biomass estimates (Figure 5A). Overall, in the analysis of relative change, the Low-flow reach had total and proportional decreases in both trout abundance (Figure 4B) and trout biomass (Figure 5B) that were greater than in the Reference reach, which suggests

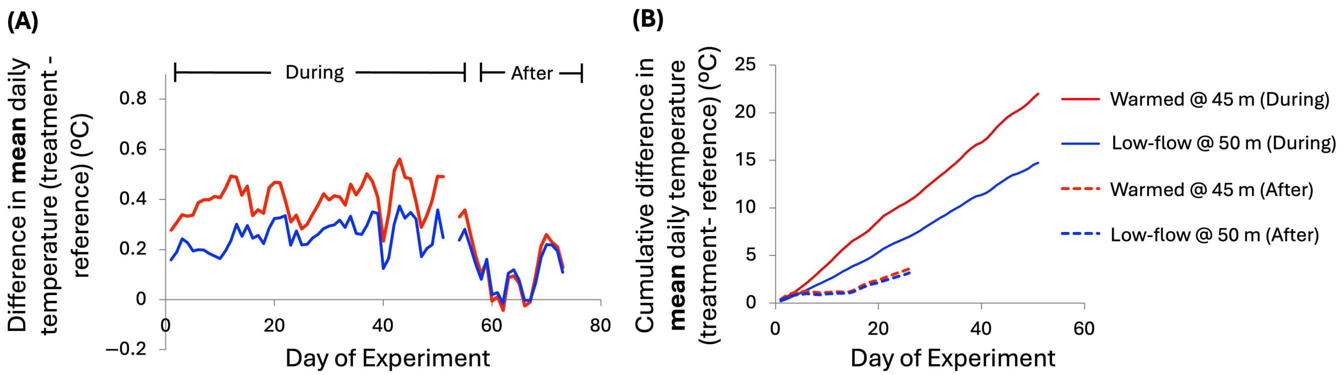

FIGURE 3 (A) Difference in mean daily temperature between the downstream locations of the Low-flow and Warmed reaches each relative to the Reference reach over the period the experiment was running ("During") and a short period following the deconstruction of the experiment ("After"). (B) Cumulative mean daily temperature (in degrees Celsius) in the Low-flow and Warmed reaches relative to the Reference reach.

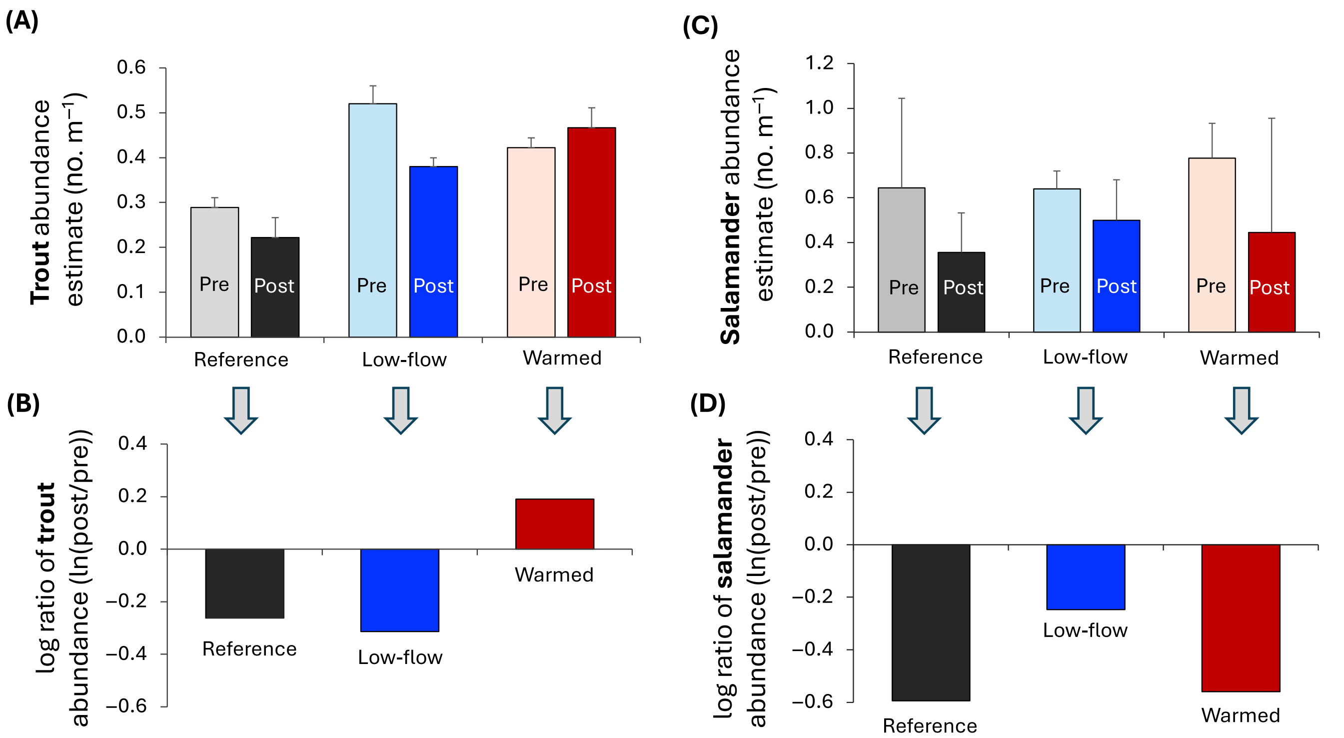

FIGURE 4 (A) Adult cutthroat trout abundance estimates per linear meter during the pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (B) Log ratios of cutthroat trout abundance between pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (C) Adult coastal giant salamander abundance estimates per linear meter during the pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (D) Log ratios of coastal giant salamander abundance between pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. Error bars in panels (A) and (C) reflect 95% CIs, with the lower bound representing the least number of captures during the sampling events. Error bars are not possible for (B) and (D) because the change between the pre-treatment and post-treatment periods includes negative values. 'Pre' refers to the conditions prior to the start of the experimental design, while 'post' represents the conditions at or during the end of the experiment.

a negative effect of decreased flows. In contrast to the Reference and Low-flow reaches, the Warmed reach had substantial increases in cutthroat trout abundance (Figure 4A) and biomass (Figure 5A) from July to September based on 95% CI overlap. Analysis of overall change relative to the Reference reach in the context of the BACI study design (quantifying change over the summer normalized to the reference site) further reinforces the positive response in trout population demographics to small increases in stream temperature (Figures 4B and 5B).

Mean trout condition during the pre-treatment period was not significantly different between the Reference and Low-flow reaches (ANOVA, $p = 0.28$; Figure 6A). However, during the pre-treatment period, mean fish condition in the Warmed reach was significantly lower than in the Reference reach (ANOVA, $p = 0.004$; Figure 6A). From July to September, mean trout condition declined by ~8.5% in the Reference reach and by ~7.8% in the Low-flow reach (ANOVA, $p = 0.17$ and $p < 0.01$ between July and September condition in REF and Low-flow reaches, respectively; Figure 6B). In contrast to the Reference and Low-flow reaches, mean trout condition in the Warmed reach increased by a small amount (~3%; Figure 6B), although this change between the pre- and post-treatment period was not significant (ANOVA, $p = 0.44$; Figure 6A). When considering the changes in trout condition factor over the summer in the treatment reaches relative to the Reference reach, there was minimal evidence for any notable response in the Low-flow reach, but a potential positive condition factor response in the Warmed reach.

Coastal giant salamander responses to the two treatments contrasted with those of cutthroat trout in regard to abundance estimates, biomass estimates, and condition factor, although due to lower capture probabilities, abundance and biomass differences were not always significant. Estimated salamander abundance and biomass declined across all three sites from July to September; however, the decline in the Low-flow reach was much smaller than in the Reference or Warmed reach (Figures 4C and 5C). The ratio analysis also indicated much smaller declines for salamanders in the Low-flow reach, and when compared against the summer change

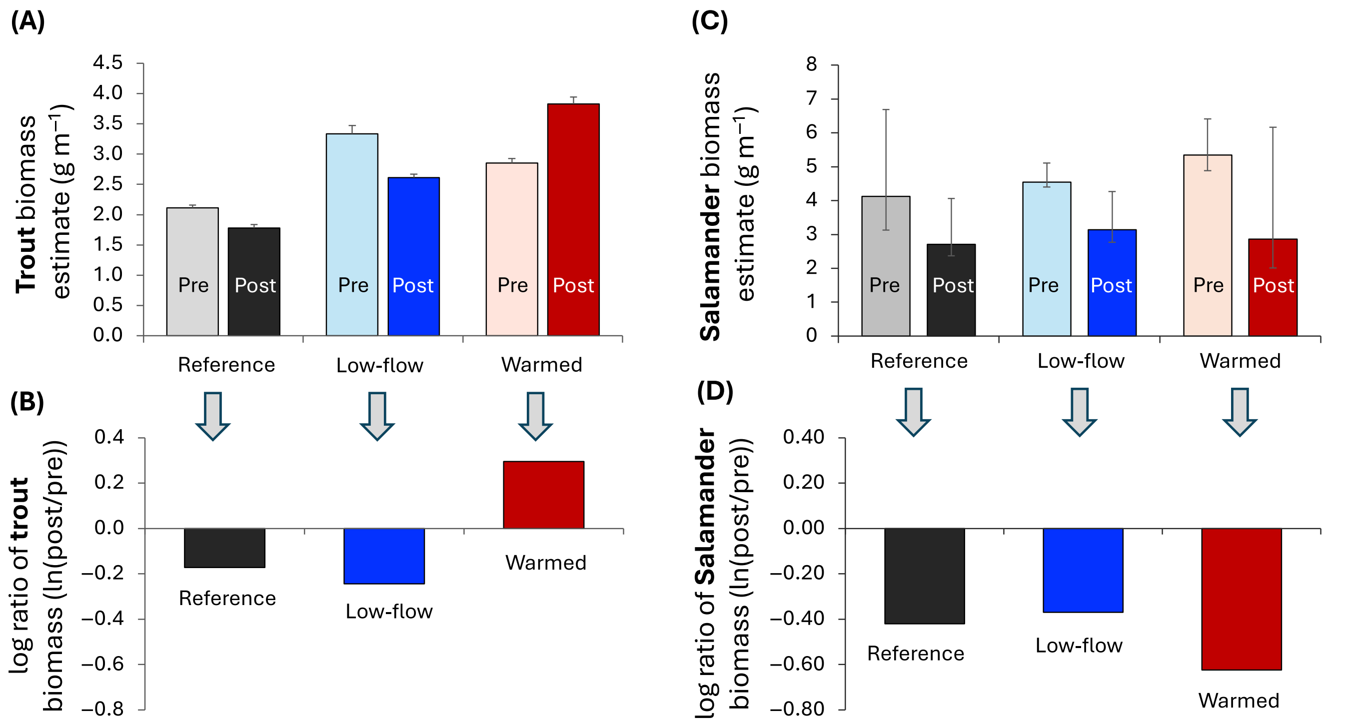

FIGURE 5 (A) Adult cutthroat trout biomass estimates during the pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (B) Log ratios of cutthroat trout biomass between pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (C) Adult coastal giant salamander biomass estimates during the pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (D) Log ratios of coastal giant salamander biomass between pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. Error bars in panels (A) and (C) reflect 95% CIs. Error bars are not possible for (B) and (D) because the change between the pre-treatment and post-treatment periods includes negative values. 'Pre' refers to the conditions prior to the start of the experimental design, while 'post' represents the conditions at or during the end of the experiment.

in the Reference reach, the change in the Low-flow reach was a relative increase (Figures 4D and 5D). Salamander condition factor increased in all reaches between July and September (Figure 6C), with smaller and comparable increases (6% and 8%) in the Reference and Warmed reaches, and a much larger increase (18%) in the Low-flow reach (Figure 6D).

Few YOY trout were captured in this study. Only one individual was captured across all reaches in July (in the Reference reach). In September, six YOY were captured in the Reference reach, five were captured in the Low-flow reach, and four were captured in the Warmed reach. The mean condition factor was lowest in the Warmed reach (0.86) and highest in the Reference reach (0.90). Mean mass of YOY was greatest in the Warmed (0.51) and lowest in the Low-flow (0.37) reaches.

The recapture of elastomer tagged trout within their originally tagged reach in September was comparable between the Reference and Warmed reaches (54% and 53%, respectively). The recapture rate for the Low-flow reach was slightly lower, but not substantially (46%). Despite increases in fish density in the Warmed reach, the apparent growth (change in mass from July to September) of recaptured PIT tagged trout in that reach was positive. The mean apparent growth of recaptured fish between July and September in the Warmed reach (0.19 g, $n = 5$) was greater than in the Reference (0.071 g, $n = 6$) and Low-flow (−0.20 g, $n = 4$) reaches, though the difference was only statistically significant between the Warmed and Low-flow reaches (ANOVA, $p = 0.02$ for Warmed vs. Low-flow and $p = 0.25$ for Warmed vs. Reference; Figure 7).

DISCUSSION

Drought events across the Pacific Northwest can have adverse effects on stream apex predator populations, such as reduced trout abundance (Arismendi et al., 2024; Kaylor et al., 2019; VerWey et al., 2018) and reduced salamander condition (Kaylor et al., 2019). However, it was not clear in those studies—or in other in situ drought studies—whether biota respond more strongly to the increases in stream temperature or to the reductions in streamflow during a drought. Furthermore, it is unclear

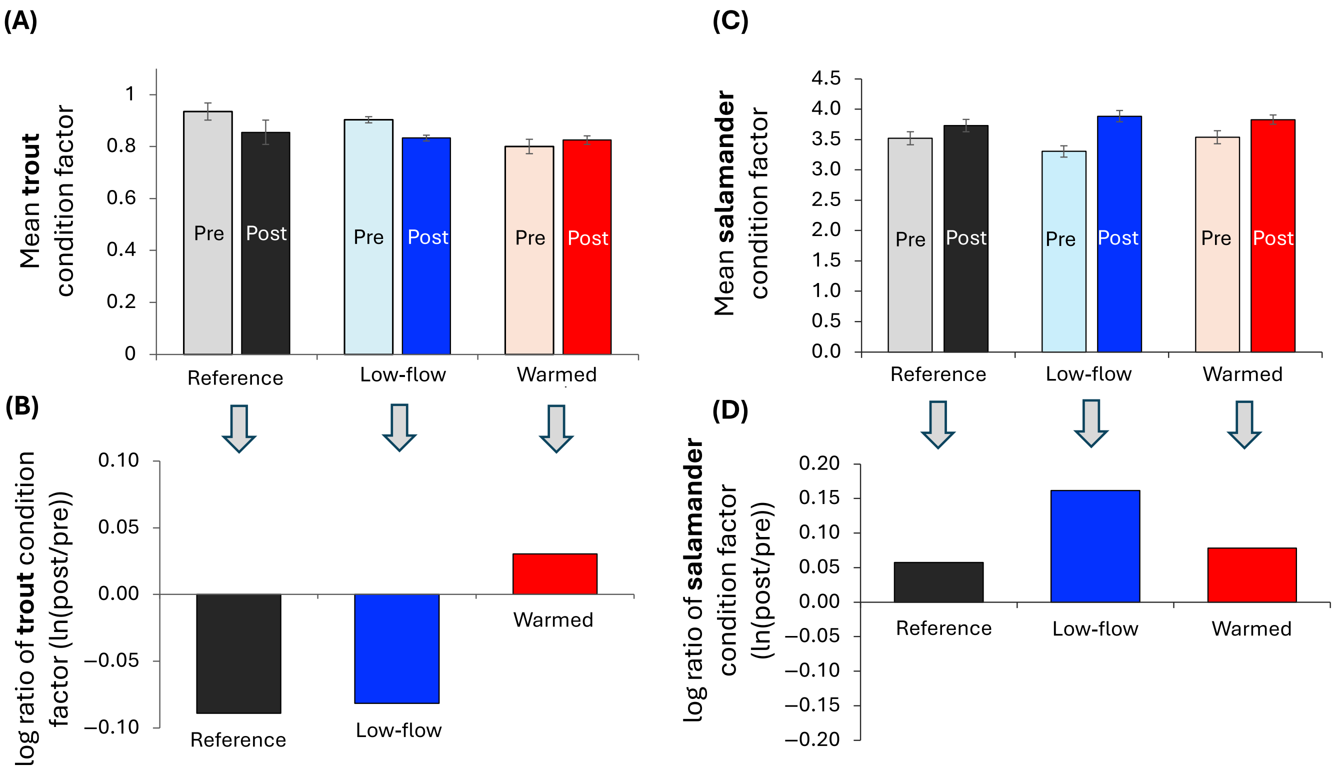

FIGURE 6 (A) Adult cutthroat trout condition factor estimates during the pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (B) Log ratios of cutthroat trout condition between pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (C) Adult coastal giant salamander condition factor estimates during the pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. (D) Log ratios of coastal giant salamander condition between pre-treatment and post-treatment surveys in the Reference, Low-flow, and Warmed reaches. Error bars in panels (A) and (C) reflect 95% CIs. Error bars are not possible for (B) and (D) because the change between the pre-treatment and post-treatment periods includes negative values. 'Pre' refers to the conditions prior to the start of the experimental design, while 'post' represents the conditions at or during the end of the experiment.

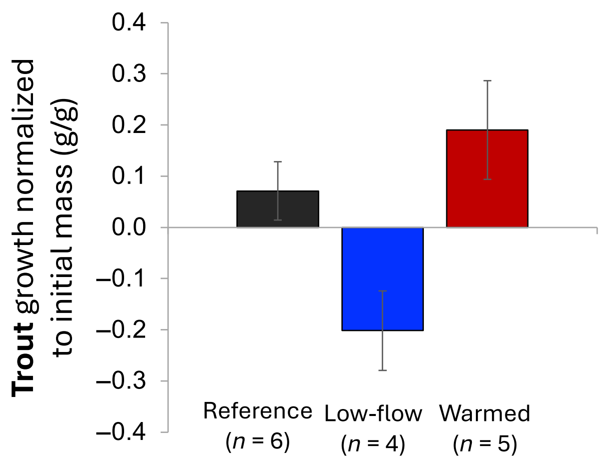

FIGURE 7 Cutthroat trout summer growth, calculated as the change in mass (post-treatment survey mass minus the pre-treatment survey mass) divided by initial mass.

how these two aspects of stream drought conditions affect the relative responses between these two key species in western headwater streams. In this experiment, we found distinct differences in the responses of trout and salamanders to reduced streamflow and moderate temperature increases. Trout abundance, biomass, and mean condition responded positively to a moderate (~0.6°C) increase in mean of the maximum daily stream temperature over the summer, as evidenced by relative increases in abundance, biomass, and mean condition for fish in the Warmed reach. Trout in this system responded negatively to reduced flows despite a slight temperature increase (~0.3°C) in the mean maximum daily summer temperature in the Low-flow. While we cannot infer mechanisms for trout declines in the Low-flow reach directly from this study, we suggest that reduced abundance and relative condition could be attributable to lower prey availability, greater negative interaction strength with conspecifics and/or salamanders, or loss of high-quality feeding and holding habitat leading to emigration and reduced growth. In contrast to trout, relative salamander abundance and condition increased in the Low-flow treatment reach and did not change (or declined very little) in the Warmed reach.

The positive response of trout abundance, condition, and growth to increased temperatures may initially seem surprising. However, in this headwater stream, initial temperatures were below the optimal growth temperatures for cutthroat trout (estimated to be 15.4–18.3°C; Rogers et al., 2022), and the applied temperature increases brought the system closer to this optimal thermal range. Therefore, the greater growth response among trout in the Warmed reach, despite higher abundance and expected increased competition, aligns with bioenergetic expectations when compared to the Reference and Low-flow reaches. Studies of optimal temperatures for growth in coastal giant salamanders are limited. However, this species is found in abundance in systems with mean summer temperatures that exceed the mean daily maximum temperatures in our focal stream (Swartz & Warren, 2023). We therefore speculate that it is more probable that inter- and intra-species interactions may have reduced salamander abundance in this reach, potentially due to greater abundance of larger trout and/or greater condition of salamanders that remained in the reach.

The increase in temperature in the Warmed reach was less than one degree Celsius. Despite this minor increase, the magnitude aligns with the temperature changes observed in this region during natural drought conditions. During the 2015 drought, the daily mean temperature in August in this stream was 14.22°C compared to the summer 2014 (non-drought year) daily mean August temperature of 13.66°C. Therefore, the 2015 drought caused stream temperatures to warm by 0.56°C relative to the 2014 non-drought year (Kaylor et al., 2019). Over the course of the 2022 summer, the Warmed reach had an overall elevated mean daily temperature of 0.43°C and an overall elevated mean daily maximum temperature of 0.61°C relative to the reference reach, therefore providing realistic treatment conditions of replicating drought-induced stream water warming.

The negative response of trout abundance, condition, and growth rates to reduced flows was consistent with other studies. Trout have previously been observed to decrease in abundance (Kraft, 1972) and exhibit reduced spring-to-fall growth (Nuhfer et al., 2017) when flow reductions occur. Not only were there fewer fish in the Low-flow reach, but they also grew less. The Low-flow reach experienced the greatest loss in pool habitat, which may explain the negative response of trout to reduced flow conditions. Although one would expect trout growth to increase under typical density dependence (i.e., fewer individuals leading to less competition for food and thus increased growth), the observed growth declines are better explained by the loss of food availability. We did not quantify the abundance of macroinvertebrate prey, but studies have found that with reduced flows, the availability of prey in the drift declines, whether benthic densities change or not, due to lower delivery rates (Uthe et al., 2019; Wilzbach et al., 1986). Salamander growth was not quantified; however, as primarily benthic feeders rather than drift feeders, they may be less likely to be impacted by reduced drift during lower flows. Additionally, since salamanders predominantly inhabit the benthic and hyporheic zones, reduced flow is less likely to inhibit their mobility. While stream flow was not completely eliminated from the Low-flow reach, the reduced flow was likely more impactful on the trout than the salamanders for this reason. Salamander abundance did decline in the Low-flow reach; however, in the BACI context where changes are evaluated relative to an unmanipulated reference reach, there was a net increase in the Low-flow reach compared to the Warmed reach.

The varying responses in condition between the salamanders and trout reflect an interplay of stream processes and species interactions that shape species-specific outcomes. In the Warmed reach, enhanced thermal conditions that prompted increased fish growth also had associated improvements in trout condition. In the Low-flow reach, decreased trout condition aligns with the reduction in growth, where we speculate lower flows likely reduced feeding opportunities in the drift. The varying response in trout condition during drought years across different reaches is consistent with findings from other research in the same region (Kaylor et al., 2019) and elsewhere (Walters, 2016). However, in decoupling the drought effects of temperature and reduced flow, we attribute the positive response in condition to warming in otherwise cool headwater streams, and we attribute negative responses to reduced streamflow. Contrary to earlier results from a study of salamanders during a severe drought in this region (Kaylor et al., 2019), salamander condition increased across all reaches in our experiment. This could be due to increased growth as benthic invertebrates become increasingly concentrated as flows declined throughout the summer. Or it could be due to differential emigration—where lower condition individuals left the treatment sites, leaving better condition individuals in the system at the end of the summer. In the future, direct assessment of salamander growth will improve our ability to capture these drivers of changing condition in decoupled drought conditions.

Decoupling temperature from flow effects of drought not only aids understanding of vertebrate responses to drought but also how trout and salamanders may respond to other disturbances that influence flow, temperature, or both. For example, headwater streams in the Pacific Northwest generally get warmer in the summer after fire due to loss of canopy cover (Beyene &

Leibowitz, 2024). But the loss of trees from the landscape also often leads to initial increases in summer streamflow (Segura et al., 2019). While we did not explicitly evaluate effects of elevated flows, trout responded more strongly to changes in reduced flow than to the moderate temperature increases that were created, highlighting the importance of flow changes for trout. Our data suggest that as long as temperatures remain below stressful levels, trout are potentially more resilient to moderate localized temperature increases than to reductions in flow. Many catchments in this region were also subject to timber harvest in the 1950s–1970s. Recent studies have found that in this context, while flows and temperature may increase somewhat initially, which suggests potential shifts toward more favorable habitat for trout, there can be a long-term legacy of decreased flows ten to fifty years after harvest (Coble et al., 2020; Segura et al., 2020). Thus, with these long-term flow declines there may be, over longer time periods, a shift toward creating conditions more favorable for salamanders. The responses in the current study highlight the ecological importance of understanding both the short and long-term flow trends in considering the future interactions of trout and salamanders in western headwater streams.

We focused on evaluating responses in the two treatment reaches relative to that of the reference reach. We focus on this to maintain a BACI design, but more fundamentally, we set the study up in a BACI framework because there is a natural decline in flow in these systems through the summer due to the Mediterranean climate. With this natural change in flow, there could be some natural background level of immigration, emigration, or death through the summer; however, the reference site was designed to address this. By having our reference as an upstream reach site, we were confident that we could capture the overall hydrologic pattern for the system better than if we had set up our reference site in a nearby stream that may have slightly different hydrogeographic characteristics. Overall, the reference site is a reference; it is not a true control in this context. We therefore assume, as all BACI studies in natural systems, that the changes in abundance or biomass in the reference site over the summer reflect probable changes that would have occurred in the treatment sites if they had remained unaltered. Further, we also assume that the act of capturing and handling fish and salamanders does not impact their survival, emigration, or growth—or if it does, that this impact is applied equally across all reaches. Given the experienced nature of the crew and the consistency in the crew members across all three reaches in the surveys, we argue that this is a robust assumption that allows for the use of the reference site data in our BACI analysis.

Large-scale manipulative field experiments require immense planning, permitting, and monitoring, and are limited due to logistical constraints. Overall, the field methods applied here for decoupling flow and temperature responses of drought were effective to test our hypotheses, but in the future, or if others look to apply this method, we recommend testing additional methods for increased warming. The passive warming in this study was effective to some degree, but larger increases in warming could be more informative. The flow diversion was effective. Because we were only creating a partial dewatering, leaks around the temporary flow diversion structure were not a major issue. While we did not evaluate movement outside of our study reaches explicitly, it is unlikely that the flow diversion influenced potential fish movement. The 10 cm pipe in the flow-through section of the seasonal diversion structure was large enough to pass any of the largest individuals in these systems. Due to PIT tag permitting restrictions, we were unable to measure salamander growth. Including salamander growth metrics from recaptured PIT tags would have provided greater confidence in explaining the observed reduction in abundance and increase in condition factor by identifying if the salamanders were indeed growing larger and fitter due to the treatments. Despite these limitations, this study highlights important localized trends and captures key differences in the response of our two focal species. Future research refining this experimental design, replicating treatments, and tagging both trout and salamanders will allow us to gain deeper insights into the mechanisms driving these species responses and interactions under decoupled drought conditions.

CONCLUSION

Overall, our experiment suggests that during drought in headwater ecosystems, reduced flows are the key driver of trout declines, and that small increases in temperature may actually provide trout a slight competitive advantage over salamanders in headwater streams (assuming temperatures remain below thermally stressful levels). Salamanders were unimpacted or even increased (relative to a reference site) in a reduced-flow environment where trout declined, and in the elevated temperature reach where trout increased, the salamanders declined. Direct conclusions about species interactions cannot be drawn from these data, but they suggest that drought conditions in headwater streams in the western United States have the potential to exacerbate interspecific competition between trout and salamanders, and we hypothesize that this competition will lead to shifts in community dynamics favoring trout under warmer conditions and salamanders under drier conditions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Maffia et al., 2024) are available from the Environmental Data Initiative (EDI) Data Portal: https://doi.org/10.6073/pasta/75ff37f814062249c02f27173e0efdce.

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