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PRIMARY RESEARCH PAPER

Drought impacts to trout and salamanders in cool, forested headwater ecosystems in the western Cascade Mountains, OR

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Abstract Climate change projections for the western United States suggest that many regions will experience increasing frequency and severity of droughts. In summer 2015, the Pacific Northwest experienced a drought with early onset of stream low flows, reduced summer discharge, and elevated temperatures. We evaluated population responses of two dominant stream predators—coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and coastal giant salamander (*Dicamptodon tenebrosus*)—across nine Cascade Mountain streams. Drought conditions impacted both trout and salamanders, but their responses differed. Adult trout abundance and biomass were significantly lower in 2015 relative to 2014, a year with discharge and temperature closer to historical norms. Juvenile trout abundance did not differ between years but juveniles were significantly larger in 2015. Salamander abundance and biomass were not significantly different between years but body condition was lower in all nine streams in 2015. Differences in temperature among streams did not explain trout or salamander responses. Habitat was important for trout responses with trout abundance and biomass experiencing smaller declines in systems with more deep pool area. Despite notable short-term drought impacts to trout and salamanders in 2015, populations recovered to pre-drought conditions within two years in all but the smallest stream.

Keywords Drought · Disturbance · Cutthroat trout · Coastal giant salamander · Climate change

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Introduction

Extended periods of abnormally low streamflow (drought) can have a severe impact on stream environments and the organisms that inhabit lotic ecosystems (Lake, 2003; Walters, 2016). Low-flow periods are typically accompanied by elevated stream temperatures, reduced habitat availability, and altered food webs (Lake, 2003; Power et al., 2013). The influence of these physical habitat changes on stream organisms is context dependent, with responses that are influenced by the species being evaluated, the severity and duration of the drought, and the availability of thermal and habitat refugia required by species (Walters, 2016). In the summer of 2015, an extreme drought occurred across northwestern North America (hereafter Pacific Northwest, "PNW") resulting in record low spring and summer discharge and elevated stream temperatures (Mote et al., 2016). We evaluated the responses of coastal cutthroat trout [*Oncorhynchus clarkii clarkii* (Richardson, 1836)] and coastal giant salamander [*Dicamptodon tenebrosus* (Baird & Girard, 1852)] across a thermal and physical habitat gradient in Cascade Mountain streams of western Oregon. Salmonid fishes and aquatic salamanders are co-dominant apex predators in many headwater streams of the PNW (Roni, 2002). While salmonid (Hakala & Hartman, 2004, James et al., 2010) and salamander (Price et al., 2012; Currinder et al., 2014) responses to drought have been evaluated independently, the responses of these two competing predators have not been evaluated concurrently in headwater streams.

The Mediterranean climate of the Cascade Mountain region of the PNW is characterized by wet winters and dry summers. This creates a regular annual summer low-flow period when temperatures reach annual maxima and flows reach annual minima, which in turn creates thermal and hydrologic constraints on available habitat for coldwater species (Arismendi et al., 2013). Climate models for the PNW suggest an expansion of this annual low-flow period as winter snowpack declines and air temperatures in spring and summer increase (Mote et al., 2003). This will lead to lower total snowmelt runoff volumes, earlier spring run-off, reduced summer flows, warmer stream temperatures, and increased frequency and severity of extreme low-flow conditions (Sproles et al., 2013; Leibowitz et al., 2014). Transition systems—those fed by a combination of snowmelt and rain—dominate mid- and high-elevation areas across the Cascade Mountains and may be particularly vulnerable to climate change (Hamlet & Lettenmaier, 1999; Mote et al., 2003; Mantua et al., 2010; Sproles et al., 2013). The response of biota to changes in these mid-elevation mountain stream environments is of particular concern as the realization of future climate projections have the greatest potential to impact thermal and hydrological conditions of coldwater species such as coastal cutthroat trout and coastal giant salamanders (Mote et al., 2003; Mantua et al., 2010; Beechie et al., 2013).

Salmonids typically exhibit negative responses to low-flow events including decreased growth rates, abundance, survival, or body condition (Hakala & Hartman, 2004; Berger & Gresswell, 2009; Walters, 2016). Salmonids may survive in pool habitats and thermal refugia during low-flow, but these are still stressful periods for coldwater biota (Matthews et al., 1994; Ebersole et al., 2003; Magoulick & Kobza, 2003; Sheldon, 2010). During annual low-flow periods, studies in the PNW have found reduced growth rates and survival relative to other seasons for resident salmonids (Berger & Gresswell, 2009; Sheldon, 2010). Increased density-dependent interactions, greater predation, reduced food availability, and increased metabolic demand may all contribute to observed reductions in growth, biomass, and survival of salmonids in headwater streams during low-flow (Power et al., 2013; Walters, 2016). However, the strength of these biotic/physiological drivers and the overall magnitude of drought and seasonal low-flow impacts on salmonids will also depend upon the thermal and physical conditions of streams. For example, populations residing in streams that remain well below a species' thermal tolerance are generally regarded as less vulnerable to temperature increases than populations inhabiting streams with temperatures closer to species' thermal tolerances (Williams et al., 2009). Similarly, in streams with more frequent or larger pools, salmonids may also be insulated to some degree from the impacts of drought and elevated summer temperatures. Sheldon (2010), for example, demonstrated that annual cutthroat trout survival was the lowest during low-flow periods and that survival was positively related to pool depth. Therefore, for stream salmonids, habitat conditions likely interact with community/food web dynamics and physiological stress responses to influence overall responses to extreme low-flow conditions.

Aquatic salamanders can generally persist in areas where flow is too low for fish, yet they have been found to be susceptible to impacts from low-flow conditions (Price et al., 2012; Brenee' et al., 2014; Currinder et al., 2014). However, in contrast to fish, salamander mobility and their unique life histories may potentially mediate the effects of drought. Many species of stream salamander, including the coastal giant salamander, are facultatively paedomorphic and can retain larval characteristics such as gills or undergo terrestrial metamorphosis and move to adjacent riparian habitats (Nussbaum & Clothier, 1973). Price et al. (2012), for example, found that aquatic larval Northern Dusky salamander [*Desmognathus fuscus* (Rafinesque, 1820)] occupancy was reduced by 30% during a drought but they suggest that this decline was due in part to metamorphosis and temporary emigration to terrestrial habitats. Ontogenetic shifts in salamanders can be triggered by environmental stimuli such as increased density dependence and competition (Werner, 1986), which are both common population level responses during droughts. Stream salamanders can also burrow into the hyporheic zone during dry periods (Feral et al., 2005) or enter underground refugia (e.g. caves; Bendik & Gluesenkamp, 2013), potentially increasing resistance to drought conditions. Independent of the mechanism (whether mortality, metamorphosis, or accessing sub-terminal refugia), a reduction in salamander abundance in stream surface waters is likely during a drought; however, to date, this potential salamander response has not been assessed empirically across multiple replicate streams in the PNW.

Droughts are unpredictable disturbances, and it is therefore difficult to plan a study specifically targeted to evaluate impacts of a natural drought. However, when pre-treatment data are available, droughts can be an effective natural experiment that allows us to explore how these disturbance events affect aquatic biota (Hakala & Hartman, 2004). We took advantage of stream monitoring that we had conducted in 2014 (and to a lesser degree 2013) across nine streams in western Oregon to serve as pre-treatment data prior to the drought of 2015. We then returned in 2016 and 2017 to evaluate short-term recovery in a subset of these sites. Our goals in this study were to (1) quantify demographical responses of cutthroat trout and coastal giant salamanders in summer during a severe drought (short-term responses), (2) determine how habitat may mediate any observed short-term responses during the drought, and (3) evaluate initial recovery (within 2 years) after a drought.

We first evaluated overall trout and salamander short-term abundance, biomass, and body condition responses to drought across nine stream sections by comparing these metrics in 2014, a year with discharge in the normal range of streamflow variability, to the severe drought year of 2015. These nine stream sections had similar species composition, geomorphology, and climate, but exhibited variable habitat conditions. This allowed us to evaluate relationships between population responses (i.e. % change in trout and salamander abundance, biomass, and condition from 2014 to 2015) and stream habitat conditions (i.e. temperature, stream size, and pool availability). We expected the total abundance and biomass of adult trout and salamanders to decrease in response to drought across all study streams, but we expected greater decreases in warmer streams relative to cooler streams. In contrast to adult trout, it has been predicted that the size and total biomass of juvenile trout may increase in PNW streams with climate change due to earlier fry emergence, a longer summer growing period, and reduced competition with adults (Penaluna et al., 2015). We therefore explicitly evaluated juvenile trout independently from adults to determine abundance, biomass, condition, and mean size responses to the drought. In the two years following the 2015 drought, we evaluated impact persistence and short-term recovery dynamics of trout and salamander biomass and conditions in five of the nine streams. Few studies have evaluated salmonid or salamander recovery from drought. However, studies that have assessed fish (Griswold et al., 1982) and salamander (Price et al., 2012) recovery from drought in headwaters suggest that recovery can be rapid. We therefore anticipated that if negative trout and salamander responses occurred during the drought of 2015, short-term recovery to pre-drought levels would occur within the two-years of post-drought sampling.

Methods

Study design and sites

The nine study streams were located in the McKenzie River drainage basin within the Western Cascade Mountains, OR (Fig. 1). Six of the streams (upper McRae Creek (MR504), lower McRae Creek (MR404), McRae Creek west tributary (MCTW), McRae Creek east tributary (MCTE), Lookout Creek upper (LO703) and Lookout Creek lower (LO701)) were located in the HJ Andrews Experimental Forest (HJA), a 6,400 ha forest encompassing the entire Lookout Creek drainage basin. Indian Creek is a tributary of the McKenzie River and is located

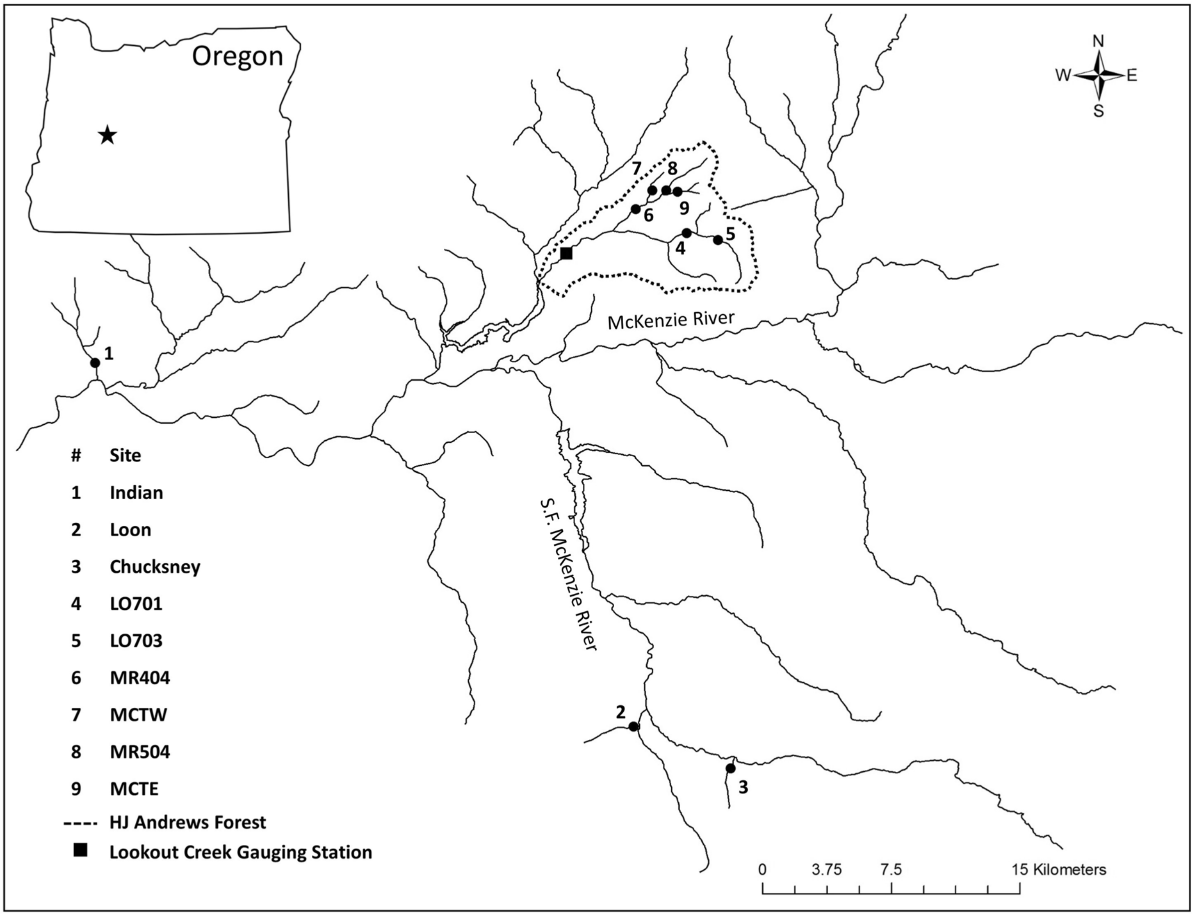


Fig. 1 Map of the nine study sites (circles) and Lookout Creek streamflow and temperature gauge (square) within the McKenzie River basin, OR

approximately 25 km west of the HJA on Bureau of Land Management (BLM) land near the town of Vida, OR. Loon Creek and an unnamed creek draining Chucksney Mountain (hereafter Chucksney Creek) are tributaries of the South Fork McKenzie River, located 28 and 30 km south of HJA, respectively, on USDA Forest Service lands upstream of the Cougar Reservoir (Fig. 1). These nine streams varied in size (3-10 m bankfull width), in percent pool area (12-42%) and in mean summer temperature (9.1–14.9°C) (Table 1), which allowed us to evaluate how physical conditions may influence species' short-term responses to drought.

To evaluate short-term fish and salamander population recovery, we resampled five of the nine streams (MCTW, MCTE, LO701, Loon Creek, and Chucknsey Creek) in 2016 and 2017. These five sites also represent a gradient of stream sizes and encompassed the smallest and largest streams of the nine primary study sites (Table 1). Logistical constraints (i.e. other experiments and wildfire) prohibited sampling MCTW in 2016 and Chucksney Creek in 2017.

Stream physical conditions

A long-term gauging station on Lookout Creek (USGS 03568933), which drains the HJ Andrews forest, allowed us to contextualize the 2015 drought relative to other sampled years (2013–2017) and long-term records (1950–2017). Flow records in July of 2015 indicate that daily discharge in 2015 was below the fifth percentile for most days, and was often the lowest on record (1950–2017) for that day of year. In contrast, during the other years of this study, July discharge at the Lookout Creek gauge usually remained above the 25th percentile. Discharge and temperature details at

Table 1 Characteristics of the nine surveyed streams in this study

Site	Elevation (m)	Bankfull width (m)	Pool area (%)	Reach length (m)	Mean summer temperature (°C)	Sampling date 2014	Sampling date 2015
LO703	900	7.4	15.4	90	9.1	8/27	8/27
LO701	810	9.0	42.4	100	10.8	9/7	9/2
MR504	840	6.6	30.8	80	12.1	8/20	8/17
MCTE	860	3.0	18.2	200	12.3	9/1	9/9
Chucksney	820	5.5	18.7	170	12.3	7/29	7/29
Loon	720	6.3	32.8	160	13.3	8/1	7/29
MCTW	860	3.7	19.2	200	13.6	8/19	8/12
MR404	630	8.6	19.2	90	14.2	8/13	8/12
Indian	300	10.0	12.9	300	14.8	7/22	7/21

Stream temperature is the mean daily mean temperature from 8/12 to 9/10 in 2015. Sampling date indicates that first day of surveys. Channel width indicates the active channel

this gauging station are presented in the supplemental material (Fig. S1).

We assessed relative summer temperatures and physical habitat metrics of each stream to evaluate how habitat may mediate trout and salamander responses to drought among streams. Temperature loggers (HOBO Pro v2) were deployed in the summer of 2015 between August and early September. Long-term temperature records from Lookout Creek indicate that this time interval typically coincides with temperatures near the annual maximum (Fig. S1). The overlapping dates in which all sensors were deployed were from 8/11 to 9/9, and this interval was used to quantify mean daily mean temperature for each stream (Table 1). Other stream habitat parameters (bankfull width, pool characteristics, and percent pool area in a reach) were collected in 2014 in accordance with other concurrent research efforts (Kaylor & Warren, 2017). No substantial storm events that would have impacted stream morphology occurred between the study years, 2014 and 2015. Bankfull width was measured at 11 evenly spaced transects in each study reach. At each pool, we measured length, width, maximum depth, and outflow depth. Percent pool area was quantified as the summed pool area divided by the total reach wetted area (wetted widths were measured in the same 11 transects concurrent with bankfull width). Sheldon (2010) demonstrated that annual cutthroat trout survival was the lowest during low-flow periods and that survival was related to pool depth up to 25 cm in which increases in depth beyond 25 cm did not correlate with increased survival. Therefore, we additionally quantified percent “deep pool area”, which we defined here as the percentage of pool area with residual depths greater than 25 cm.

Fish and salamander surveys

Coastal cutthroat trout and coastal giant salamanders, the two dominant vertebrates, were sampled using a backpack electrofisher (Smith-Root model LR-20B) between 7/22 and 9/7 in each year (Table 1). For each site, the date of the 2015–2017 surveys occurred within 8 days of when that site was sampled in 2014. At smaller streams—Loon, Chucksney, MCTW, MCTE and Indian—population abundance was estimated using multiple-pass depletion estimation with three successive, equal effort passes (Hauer & Lamberti, 2007). Stream reaches were blocked on both ends with nets to ensure a closed population during multiple-pass depletion sampling. Captured trout and salamanders were held in aerated containers until all passes were complete. All fish and salamanders were measured (mm) and weighed (0.1 g) prior to release. Mark-recapture sampling was used at larger streams—MR404, LO701, LO703, and MR504—in which each site was sampled twice over 2 days. During mark-recapture surveys, fish were marked using a caudal clip and salamanders were marked with a visual elastomer tag (Northwest Marine Technology, Shaw Island, Washington). After measuring, weighing and marking, individuals were released within the netted reach and captured approximately 24 h later.

Statistical analysis

Trout and salamander abundance from multiple-pass depletion surveys were estimated using maximum likelihood estimation (Carle & Strub, 1978) and the program Microfish (v3.0; Van Deventer & Platts, 1989). Trout and salamander abundance from mark-recapture surveys were estimated using the Chapman modification of the Lincoln-Peterson mark-recapture model (Chapman, 1951). Abundance estimates and 95% confidence intervals were multiplied by mean weight to obtain biomass estimates and confidence intervals. The same body condition (K) equation was used for trout and salamanders:

$$K = \frac{W}{L^3} \times 100$$

where W is wet weight (g) of each fish or salamander and L is length (cm) expressed as total length for trout and snout-vent length (SVL) for salamanders. Juvenile (age-0) cutthroat trout abundance and biomass were estimated separately from age-1 + trout.

To compare overall population metrics (trout and salamander abundance, biomass, and condition) between 2014 and 2015, we used linear mixed effects models with a random effect corresponding to site to account for non-independent error associated with spatial dependence. Six of the sites were close in proximity (within the HJA) relative to the three other sites. To evaluate potential additional spatial dependence of sites within the HJA compared to sites outside of the HJA, we also evaluated models with random effects corresponding to site nested within basin (HJA or non HJA). Comparison of these models revealed no significant difference (ANOVA, $P > 0.05$) between models structures and $\mathrm{AIC_c}$ values were always lower for models with site as the only random effect. In addition, while six of the streams are closer in proximity, all nine streams are in the same larger basin draining the west slope of the Cascade Mountains and are within 30 km of each other with similar geomorphology, climate, and species composition across sites. We therefore proceeded with analyses with a model structure consisting of site as the only random effect. Year (2014, 2015) was included in models as a binary (0,1) indicator variable. All models were fit using the lme4 package (Bates et al., 2015) in the program R (v 3.4.3; R Core Team, 2015). Response variables were abundance (# m^{-1}), biomass (g m^{-1}), and body condition (mean) for adult trout, juvenile trout, and salamanders. We additionally evaluated mean length as a response variable for juvenile trout. Juvenile cutthroat trout occupy different habitats than adults (Moore & Gregory, 1988a) and typically exhibit positive growth rates during summer (Kaylor & Warren, 2017) while adults often lose body mass (VerWey et al., 2018). To assess differences in response metrics within a specific site between 2014 and 2015, we evaluated whether or not the 95% confidence intervals overlapped. Fish population estimates from small streams often produce 95% confidence intervals that are asymmetric because the lower bound of the confidence interval is adjusted based on the known number of fish sampled (e.g. the estimated lower confidence bound is smaller than the actual number of fish sampled and is therefore adjusted). A comparison on error bar overlap is an accepted method to evaluate differences over time in this case (Warren & Kraft, 2003; Baldigo et al., 2008).

We used linear regression to evaluate the degree to which physical habitat conditions explained observed variation in biotic response metrics during the drought year (% change in abundance and biomass of fish and salamanders from 2014 and 2015). Abiotic explanatory variables included relative summer stream temperature, bankfull width, percent pool area and percent deep pool area. Assumptions of normality and constant variance of the residuals from each model were checked graphically, and percent pool area and percent deep pool area were natural log-transformed prior to analysis to achieve normality.

Potential short-term (within two years) recovery responses of trout and salamanders from the 2015 drought were evaluated in each of five streams. Abundance and biomass responses were similar for adult trout and salamanders, and we therefore focused analyses for recovery only on biomass. This reduced analysis redundancy and in turn the potential for these additional multiple analytical comparisons to confound assessments of significance based on a set alpha value. If an initial decrease in biomass or condition was observed in 2015, we defined recovery as a return to values with confidence intervals that overlapped with confidence intervals of pre-drought years.

Results

Short-term drought impacts (2014–2015)

Adult (age-1 +) cutthroat trout abundance and biomass were significantly lower in 2015 compared to 2014 ($P = 0.003$ and 0.015, respectively; Table 2). Mean trout abundance across all sites declined by 30% ($n = 9$; SD = 18.6%) and mean trout biomass declined by 29% ($n = 9$; SD = 19.9%) from 2014 to 2015. Considering each stream individually, both adult trout abundance and biomass estimates were significantly lower (non-overlapping 95% confidence intervals) in seven of the nine surveyed streams (Fig. 2A, B). In contrast, across all sites, trout body condition was not significantly different between years ($P = 0.48$; Table 2). Trout body condition was lower in seven of nine streams in 2015, but 95% confidence intervals overlapped in all nine streams (Fig. 2C). Juvenile (age-0) cutthroat trout were substantially larger (total length; $p = 0.003$; Fig. 3A), averaging 9.9% greater length in 2015 compared to 2014 ($n = 9$; SD = 6.7%). Consequently, total juvenile biomass was significantly greater in 2015 ($P = 0.006$; Table 2). In contrast to adult trout, juvenile trout abundance was greater in six of nine streams in 2015 (Fig. 3B); however, this result was not significant when evaluated across all streams ($P = 0.106$; Table 2).

Salamander abundance and total biomass did not exhibit a clear trend and were not significantly different between years when considering all sites in aggregate ($P > 0.05$; Table 2). Salamander abundance estimates were lower in five streams but greater in four streams in 2015 compared to 2014 with overlapping 95% confidence intervals for eight of nine streams (Fig. 2D). Similarly, salamander biomass was lower in four streams and greater in five streams in 2015 and 95% confidence intervals overlapped in eight of nine streams (Fig. 2E). However, mean body condition across all streams was significantly lower for salamanders ($P < 0.001$; Fig. 2F), averaging 15.8% lower in 2015 compared to 2014 ($n = 9$; SD = 5.2).

2014–2015 habitat–response relationships

The nine streams surveyed in this study exhibited a range of summer mean daily temperatures between 9.1 and 14.9°C in the drought year of 2015 (Table 1). We expected to find relationships between relative temperature and trout population responses between years (assessed as percent change from 2014 to 2015); however, relative summer temperature was only weakly correlated with the percent change in trout abundance ($P > 0.1$; $r^2 = 0.16$) and biomass ($P > 0.1$; $r^2 = 0.05$; Fig. 4A). Even in the two coldest sites, LO703 and LO701, trout biomass was substantially reduced in 2015 and these differences were similar in magnitude to those observed at other, warmer streams.

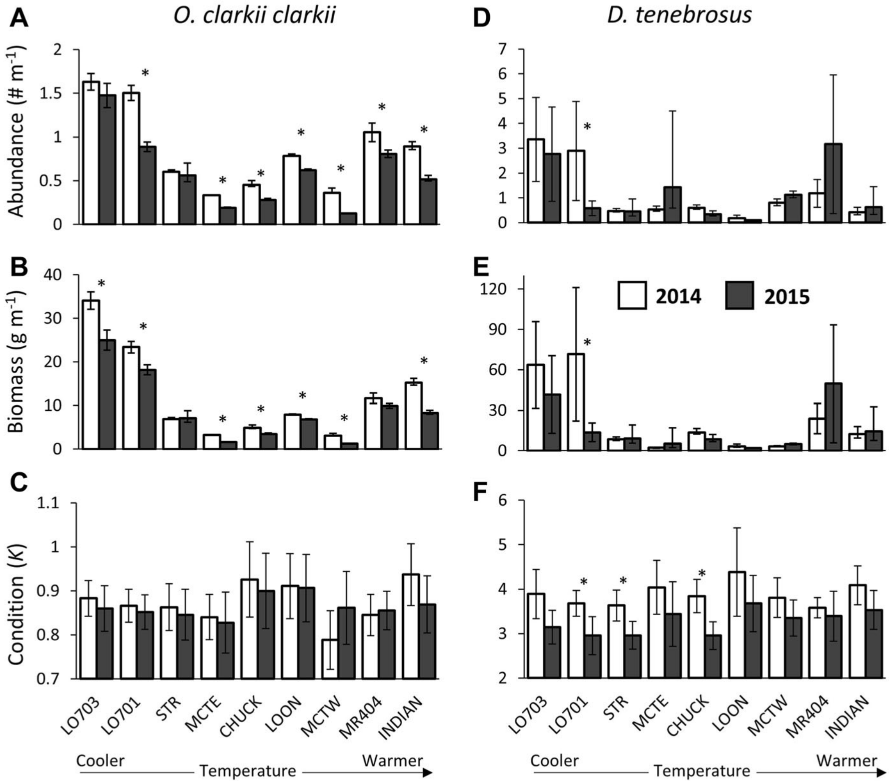
We also examined relationships between habitat metrics (bankfull width, pool area, and deep pool area) and the percent change (2014–2015) in adult trout and

Table 2 Population metrics in 2014 and 2015 and mixed effects model estimates comparing parameter estimates between years

Species	Parameter	2014	2015	Model estimate	P value
Adult cutthroat trout	Abundance (# m^{-1})	0.84 (0.16)	0.61 (0.14)	− 0.24 (0.06)	**0.003**
	Biomass (g m^{-1})	12.26 (3.49)	9.05 (2.62)	− 3.21 (1.04)	**0.015**
	Body condition	0.873 (0.016)	0.864 (0.008)	− 0.009 (0.012)	0.481
Juvenile cutthroat trout	Abundance (# m^{-1})	0.45 (0.16)	0.58 (0.14)	0.132 (0.07)	0.106
	Biomass (g m^{-1})	0.46 (0.18)	0.76 (0.23)	0.304 (0.08)	**0.006**
	Body condition	0.933 (0.037)	0.937 (0.149)	0.005 (0.031)	0.883
	Total length (mm)	44.87 (2.13)	49.27 (2.49)	4.40 (1.03)	**0.003**
Coastal giant salamanders	Abundance (# m^{-1})	1.16 (0.38)	1.18 (0.36)	0.018 (0.38)	0.963
	Biomass (g m^{-1})	22.40 (8.85)	16.56 (5.69)	− 5.846 (7.68)	0.468
	Body condition	3.883 (0.085)	3.266 (0.091)	− 0.617 (0.067)	**< 0.0001**

Parentheses indicate standard error. The model estimate is the estimated difference from 2014 to 2015 of parameter (×) using general linear mixed models

Fig. 2 Abundance, biomass, and body condition for coastal cutthroat trout (*O. clarkii clarkii*) and coastal giant salamander (*D. tenebrosus*) in 2014 (open bars) and 2015 (shaded bars). Error bars represent 95% confidence intervals and asterisks indicate non-overlapping 95% confidence intervals between years



salamander abundance and biomass across the nine streams (Table S1). The percent change in trout abundance and biomass was generally more negative in smaller streams compared to larger streams resulting in a weak positive association with bankfull width ($r^2 = 0.10$ and 0.14, respectively; Fig. 4B). Decreases in trout abundance and biomass were also greater in streams with limited pool habitat compared to streams where pools were more common, resulting in a positive association with percent pool area ($r^2 = 0.04$ and 0.33, respectively); however, the associations with deep pool area were stronger for abundance and biomass responses ($r^2 = 0.20$ and 0.55, respectively; Fig. 4C). The only significant relationship predicting percent change in trout abundance or biomass at $\alpha = 0.05$ was the relationship between deep pool area and change in cutthroat trout biomass (Table S1). Percent change in salamander abundance and biomass were positively associated with relative temperature ($r^2 = 0.22$ and 0.20, respectively), negatively associated with bankfull width ($r^2 = 0.04$ and 0.16, respectively), negatively associated with pool area ($r^2 = 0.26$ and 0.20, respectively), and negatively associated with deep pool area ($r^2 = 0.30$ and 0.30, respectively). There were no significant relationships between explanatory variables and change in salamander abundance and biomass at $\alpha = 0.05$ (Table S1).

Drought recovery (2013–2017)

We utilized data from 2013 to 2017 in five of the nine streams where short-term responses (2014–2015) were quantified to determine short-term recovery (2016–2017) of trout and salamander biomass, abundance, and body condition to the 2015 drought. In all five streams, trout biomass was lower in 2015 relative to the pre-drought years of 2013 and 2014 (based on an assessment of 95% CI overlap). However, by either 2016 or 2017, trout biomass had recovered to levels similar to or greater than pre-drought levels in four of the five streams (Fig. 5A). In the smallest stream (MCTE), biomass continued to decline in 2016 and still remained far lower than 2014 levels in 2017. We

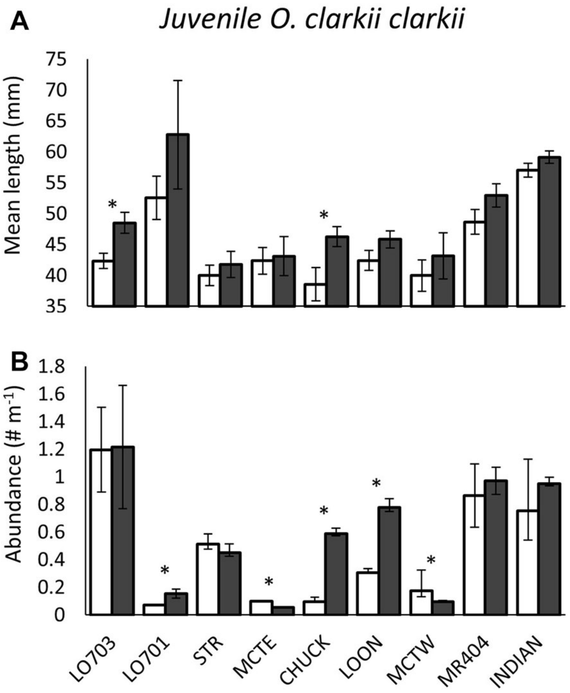


Fig. 3 Mean total length (mm) and abundance of juvenile (age-0) cutthroat trout (*O. clarkii clarkii*) in 2014 (open bars) and 2015 (shaded bars). Error bars represent 95% confidence intervals. Asterisks indicate non-overlapping confidence intervals between years within a stream

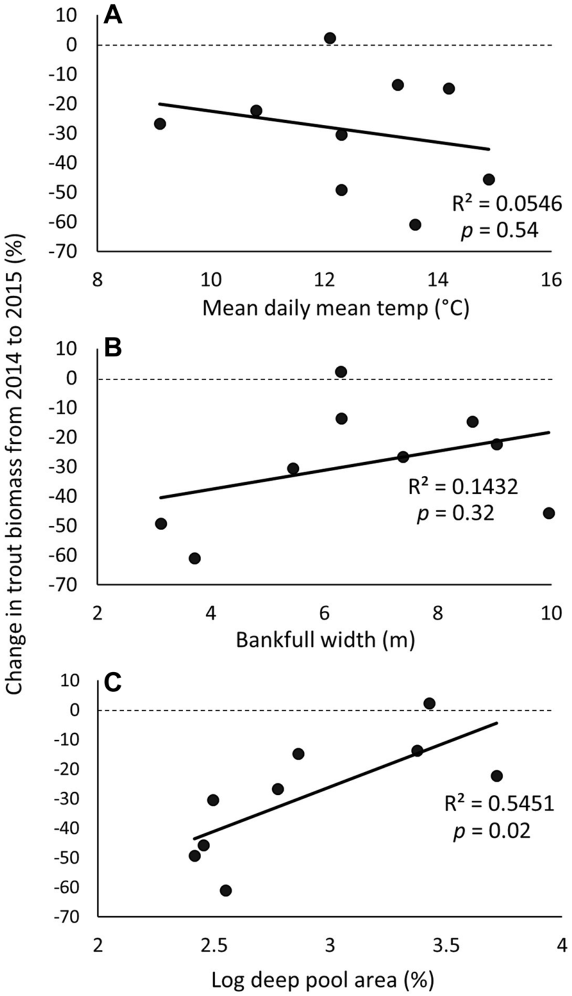


Fig. 4 Relationships between **A** daily mean temperature, **B** bankfull width, and **C** percent deep pool area relative to the percent change in reach-scale trout biomass from 2014 (non-drought) to 2015 (drought). Deep pools were classified as those with residual depth greater than 25 cm based on findings of Sheldon (2010)

did not detect any clear trends in body condition over time (Fig. 5B).

Salamander biomass responses to the drought year of 2015 were mixed, as were trends in the post-drought years of 2016 and 2017 (Fig. 6A). Trends in salamander body condition, however, exhibited a distinct recovery from their decline in 2015. Mean body condition was lower in the drought year in all five streams relative to pre-drought years, but by 2016 or 2017, body condition increased and was similar to pre-drought levels in all five streams. Data were excluded from Loon Creek in 2013 and 2017 for the condition analysis due to inadequate sample sizes to estimate body condition ($n < 10$).

Discussion

In 2015, the abnormally warm winter temperatures, low snowpack accumulation, and limited late-spring precipitation resulted in record low spring and summer discharge across the PNW (https://water.usgs.gov/data). The drought conditions observed in 2015 are anticipated to become more prevalent in montane headwater ecosystems in the future due to climate change (Mote et al., 2003, 2016). Therefore, the 2015 drought provided a rare opportunity to explore potential responses of two dominant stream predators to these conditions. We found that adult trout and salamanders both responded negatively to the drought, but the nature of the response and the magnitude of the impact differed between these headwater predators. The overall abundance and biomass of trout declined

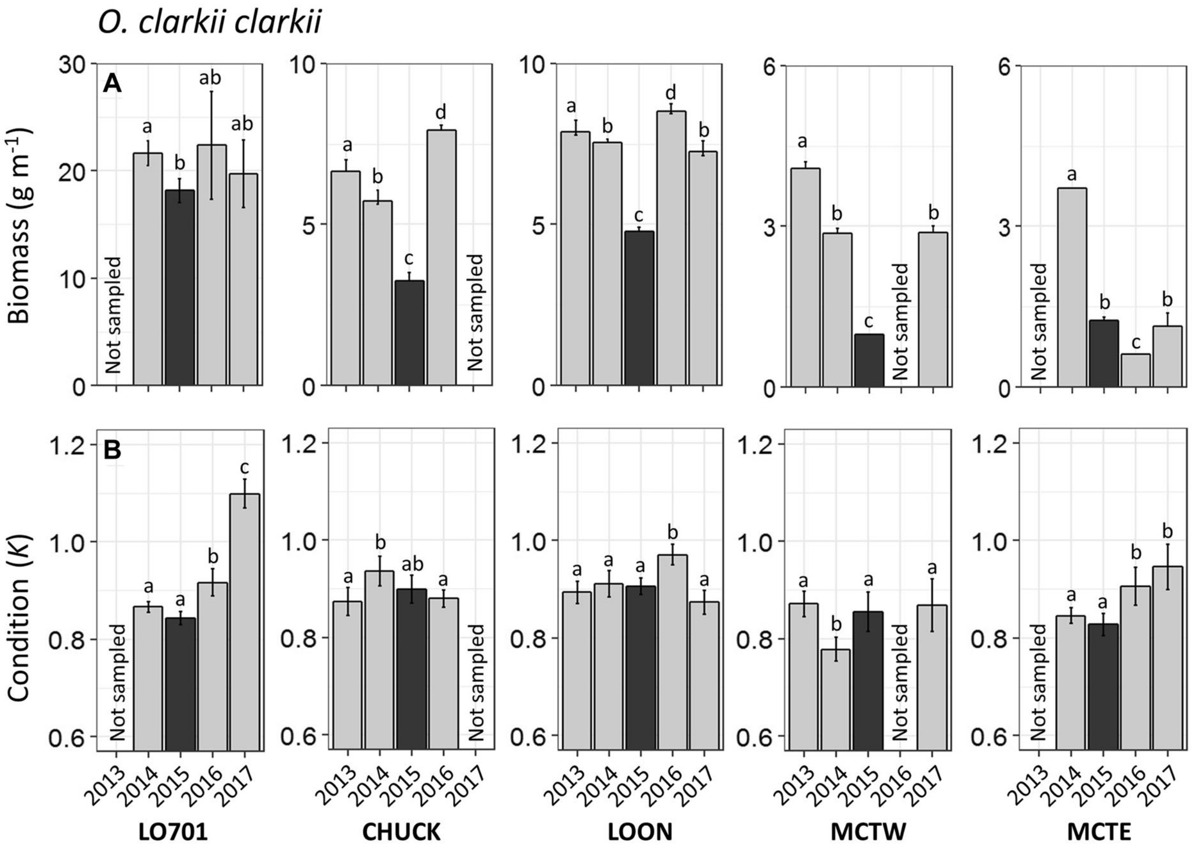


Fig. 5 Cutthroat trout (*O. clarkii clarkii*) biomass estimates with 95% confidence intervals of population estimates (**A**) and mean body condition with 95% confidence intervals (**B**) in five streams for the years 2013–2017. The darker shade indicates the drought year of 2015. Different lower-case letters above the bars within a site indicate significant differences based non-overlapping 95% confidence intervals. Bars with the same letter have overlapping 95% confidence intervals

in most streams during the drought year, but there were no systematic changes in total salamander abundance or biomass. In contrast, salamander body condition declined in all sites, while adult trout body condition was more variable with no consistent trend across all sites. In contrast to our expectations, stream temperature was not strongly associated with short-term trout or salamander responses to the drought. All of the streams studied here were relatively cool and generally remained below thermally stressful levels for most coldwater biota. Therefore, increases in temperature during drought are not likely to be the driver of different population responses among our study streams as would be expected in systems where temperatures are pushed beyond thermal tolerance thresholds (Williams et al., 2009). However, results indicate that stream pool habitat was important for trout as stream sections with more deep pools experienced smaller reductions in trout abundance and trout biomass. This result is consistent with studies that have found pools serve as important refugia for salmonids during low-flow periods (Elliott, 2000; Sheldon, 2010) and highlights the potential importance of habitat features that provide or enhance refugia for salmonids during drought conditions. Despite negative short-term trout and salamander responses to the drought, in most streams, trout biomass and salamander condition recovered within two years after the disturbance. Cumulatively, our results indicate that in these headwater ecosystems, trout and salamanders are indeed impacted by drought, but they also demonstrate the potential for populations to quickly rebound if flows and temperatures recover in subsequent years.

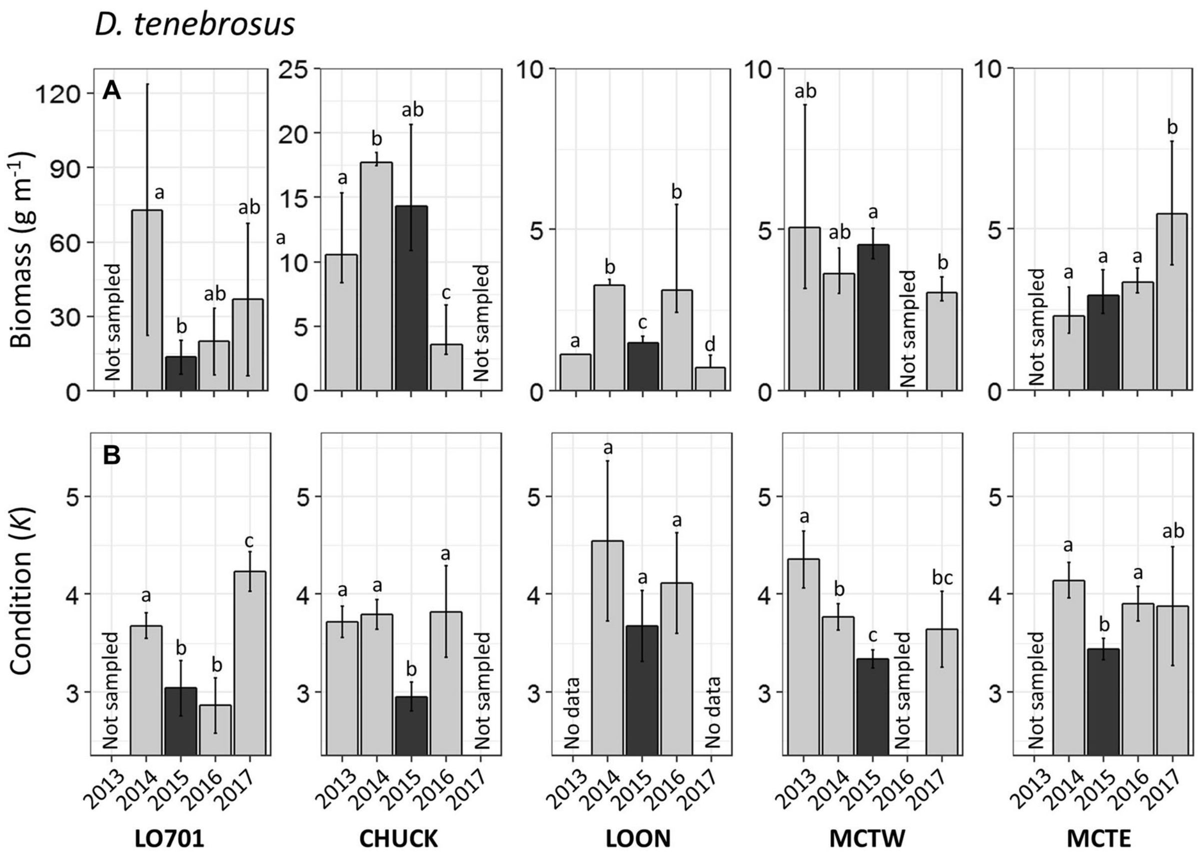


Fig. 6 Coastal giant salamander (*D. tenebrosus*) biomass estimates with 95% confidence intervals of population estimates (**A**) and mean body condition with 95% confidence intervals (**B**) in five streams for the years 2013–2017. The darker shade indicates the drought year of 2015. Different lower-case letters above the bars within a site indicate significant differences based non-overlapping 95% confidence intervals. Bars with the same letter have overlapping 95% confidence intervals

Adult cutthroat trout abundance and biomass both decreased by around 30% on average from 2014 to 2015, yet condition was not significantly different between years. Reduced abundance and biomass are consistent with a meta-analysis of studies evaluating fish responses (not exclusively salmonids) to low-flow events (Walters, 2016), as well as studies focused on salmonid responses. In contrast, a lack of change in body condition was somewhat unexpected as 65% studies evaluating fish responses to low-flow reported decreased body condition (Walters, 2016). Hakala & Hartman (2004) found that adult brook trout [*Salvelinus fontinalis* (Mitchill, 1814)] abundance decreased by 60% in response to a severe and sustained drought, and that this response was accompanied by decreased condition. James et al. (2010) also found that adult brown trout (*Salmo trutta* Linnaeus, 1758) population biomass decreased between 66% and 80% in response to drought, but no changes in condition were observed. Walters (2016) suggest that the variable condition responses in these two studies may be attributed to stream warming that accompanied reduced discharge in streams evaluated by Hakala & Hartman (2004), whereas warming was not observed in James et al. (2010). In our study streams, warming likely occurred across all streams during the drought year, yet temperatures remained below physiological thresholds. In addition, some stream exhibited reduced abundance, which may have increased resource availability for individuals and thereby reduced density dependence effects on condition. Alternatively, fish with lower body condition may exhibit higher mortality or movement out of study reaches, and therefore fish with the lowest body condition may not be sampled (Hilderbrand & Kershner, 2004).

Trout abundance and biomass recovered to pre-drought levels within two years in four of the five streams we evaluated, suggesting drought impacts were short-lived at the reach scale. The exception to this trend was the smallest stream in this study (MCTE). Trout biomass continued to decline through 2016 in MCTE and, although a slight increase was observed from 2016 to 2017, biomass remained just a third of pre-drought levels in 2017. We suggest the lack of a short-term trout biomass recovery in this stream is attributable to limited connectivity with other populations and poor juvenile recruitment—two important factors regulating the recovery responses of biota from disturbance (Lake, 2003). A steep cascade approximately 100 m downstream of our study reach likely limits cutthroat trout movement from downstream habitats, and just 300 m upstream from the study reach marks the upstream extent of trout. Therefore, the capacity to repopulate this section from upstream and downstream areas was limited. Additionally, in contrast to the larger stream sites, the number of juvenile trout observed in this section was low from 2014 to 2017, suggesting recruitment within this section was insufficient to rapidly restore adult numbers and total biomass in subsequent years. Recovery of trout abundance and biomass in this stream section may occur over longer temporal scales if there are no other substantial droughts, but this site is clearly more susceptible to repeated droughts. Interestingly, while trout biomass in MCTE remained suppressed, salamander biomass in this section consistently increased from 2015 to 2017. Because salamanders and trout may feed on similar resources in these small headwaters (e.g. aquatic invertebrates), reduced interspecific competition for resources may have allowed salamander biomass to increase after the initial disturbance had passed. The increases in salamander biomass may further complicate trout recovery processes in this stream. The results from MCTE suggest that in the smallest headwaters near the upstream extent of fish occupation, droughts or sustained reduced streamflow may facilitate shifts in the proportion of total vertebrate biomass towards salamanders, while periods of sustained flows closer to historical norms may increase the proportion of trout compared to salamanders.

Resident salmonid populations in cooler streams are generally regarded as less vulnerable to drought and climate change effects than populations residing in streams closer to species thermal tolerances (Williams et al., 2015). We therefore predicted greater relative decreases in trout abundance and biomass from 2014 to 2015 in warmer sites relative to cooler sites. However, the percent change in adult trout abundance and biomass among streams did not appear to be temperature-driven across the streams we evaluated. Streams in this study were relatively cool with mid-summer mean temperatures ranging from 9 to 15°C, even in the drought year of 2015. Therefore, background temperature may be less important as an area of focus in these systems relative to those where streams reach higher temperatures in summer. Further, the streams we sampled here may have also been buffered against multiple stressors that likely compound the effects of reduced flow to impact trout populations (e.g. habitat degradation and invasive species; Williams et al., 2015). Sampled streams contained no invasive fish species, and while logging occurred in these streams between 40 and 50 years prior, pool area has generally recovered to levels similar to reference old-growth conditions (Kaylor & Warren, 2018). Nonetheless, trout abundance and biomass consistently decreased in these cool headwaters, suggesting that biota in these systems may remain vulnerable to temperature and hydrologic changes anticipated with climate change—even if thermal regimes remain below key thresholds.

Our analyses suggest that the amount of deep pool area may be an important factor influencing the vulnerability of cutthroat trout to drought conditions. Percent deep pool area (residual pool depth > 25 cm) within a reach explained 55% of the variations in the percent changes in adult cutthroat biomass from 2014 to 2015. Reaches with greater deep pool area exhibited smaller changes in trout biomass from 2014 to 2015 than those with limited deep pool area. Pools minimize costs associated with swimming, provide thermal refugia, and provide cover from avian predators (Fausch, 1984; Matthews et al., 1994) and may mitigate negative population and physiological impacts during droughts (Elliott, 2000). These results are consistent with other studies that have found greater resident trout densities, growth rates, and survival rates in deep pools. For example, Sheldon (2010) found that pool depth was related to cutthroat trout summer survival rates with an asymptote in the depth-to-survival relationship once depths exceeded 25 cm. Similarly, May & Lee (2004) found that changes in pool depth over the summer were related to changes in cutthroat trout density and survival; greater decreases in pool depth over the summer translated to reduced survival and density relative to sections where pool depth remained more stable. Therefore, the relationship that we observed between pool depth and drought impact on trout populations may in part be attributed to differences in survival between 2014 and 2015 in reaches with varying amounts of deep pool area. In addition to survival, trout emigration rates may also be affected by the amount of deep pool areas, with more individuals leaving systems with limited deep pool refuge area. Deep pool habitat has been well established as a key habitat feature for salmonids in a general sense and, therefore, many restoration efforts target increases in pool area (Roni, 2002; Roni et al., 2008). Our results further support that deep pools may be important for cutthroat trout survival during low flows and may increase the resistance of resident trout populations to drought conditions and anticipated thermal and hydrologic alteration associated with climate change.

Juvenile cutthroat trout abundance did not decrease during the drought and juvenile trout were larger in all nine streams in the drought year of 2015. After spring emergence, juveniles occupy lateral habitats and the amount of this stream side habitat has been linked to juvenile abundance (Moore & Gregory, 1988a, b). Lower discharge in 2015 likely reduced available lateral and shallow side channel habitat, but other factors such as higher egg survival due to the absence of streambed scour during spring runoff and enhanced growth and survival after emergence may have counterbalanced changes in lateral habitat. Because densities of juveniles were not significantly lower between years in all but the two smallest streams, and because juveniles and adults typically occupy different habitats during mid-summer (Moore & Gregory, 1988a), the larger size of juveniles in 2015 does not appear to be the result of decreased density dependence. It is probable that warmer stream temperatures, and thus faster accrual of degree days in the spring of 2015, may have resulted in earlier emergence and a longer growing season. Consequently, juvenile trout sampled on or around the same day would be larger in 2015. In addition, assuming food resources were adequate for juvenile trout, warmer temperatures could have increased growth rates even if emergence times were comparable. Ultimately, it is likely that a combination of these factors resulted in larger individuals during the same survey period in mid-summer in 2015. These results provide empirical support for modelling efforts predicting larger size and greater biomass of juvenile cutthroat trout under future climate conditions (Penaluna et al., 2015). The larger juvenile trout and a general lack of drought impact on juvenile abundance may have facilitated the rapid recovery in trout abundance and biomass observed in many of the streams 1–2 years after the drought.

In contrast to adult trout responses, coastal giant salamander abundance and biomass were not significantly different between the drought year (2015) and the previous year (2014), nor were trends apparent in the two years following the drought (2016–2017). Capture probabilities of salamanders were low in all years resulting in large confidence intervals on population estimates, which limits our ability to assess population responses between years. Nonetheless, population estimates in 2015 were lower in some streams and greater in others relative to 2014, suggesting no synchronous trend in these metrics. These results contrast with a number of studies that have demonstrated reduced salamander abundance in response to drought conditions. For example, Currinder et al. (2014) found that the abundance of the most common salamander species decreased by nearly half in response to experimental drought conditions. Similarly, Price et al. (2012) found decreased juvenile salamander (*Desmognathus fuscus*) occupancy during a severe drought, which was partly attributed to temporary emigration to subsurface or terrestrial environments. Despite the abundance of salamanders in PNW streams, coastal giant salamanders have not been given the same attention as trout, and the effects of drought on this species in this region are poorly known. Further research examining longitudinal stream movements, hyporheic habitat use, metamorphosis rates, and the effect of trout presence on salamander population dynamics during drought conditions will contribute to understanding annual population fluctuations for this species and how changes in response to drought fit in this larger context.

Evaluating abundance or biomass alone would suggest that there were no consistent drought effects on salamanders; however, salamander body condition was consistently lower across all nine streams in 2015. This highlights the importance of looking beyond abundance and evaluating how effects of disturbance events may manifest as non-lethal fitness responses. Indeed, in a system from the southeastern United States, a similar reduction in stream salamander body condition was observed in a study where flows were experimentally reduced (Currinder et al., 2014). A reduction in body condition during droughts may reflect adaptation to consume energy reserves during periods of stress. For example, salamanders have been shown to exhibit tail shrinkage during droughts, presumably due to consumption of energy reserves, but then resume growth when drought conditions subside (Bendik & Gluesenkamp, 2013). Salamanders may also exhibit adaptive traits to droughts through metamorphosis and movement to terrestrial environments, which may be triggered by stressful conditions (Werner, 1986; Price et al., 2012). In the streams we evaluated, it is unclear whether body condition changes influenced short-term salamander movement and survival. However, body condition quickly returned to levels similar to pre-drought conditions, suggesting potential resilience of salamanders to drought. Further research is needed to determine how salamander life-history, survival, and movement, respond to reduced summer discharge.

Conclusions

Climate change projections for the PNW and many temperate montane regions suggest that we will see reduction in mid-elevation snowpack with earlier onset of snowmelt, resulting in reduced summer streamflow and warmer stream temperatures (Mantua et al., 2010; Sproles et al., 2013). In the PNW, reduced summer discharge and increased synchrony of minimum flow with maximum temperature are considered major threats to the persistence of biota in headwater streams (Mote et al., 2003; Arismendi et al., 2013). The two dominant vertebrate predators in the headwater ecosystems evaluated in this study both responded negatively to drought; however, these effects manifested differently. Across all streams, trout abundance and biomass decreased by approximately 30% in response to the 2015 drought. Juvenile trout, however, were larger without a systematic decline in abundance during the drought year. Although we did not observe a consistent decline in salamander abundances during the 2015 drought, salamander body condition was lower across all streams, indicating that conditions were indeed stressful for this species. Therefore, rather than identifying clear "winners" and "losers" in a future climate scenario, our results suggest that the dominant predators in the headwater streams we evaluated will have different degrees of negative responses to drought. Yet, in these coldwater streams, trout responses appear to be mediated by deep water refuge habitat and network connectivity more than by temperature alone. Maintaining these habitat features may increase the capacity of trout populations to resist future changes in hydrologic conditions.

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