Trout Under Drought: A Long-Term Study of Annual Growth and Condition of Stream-Living Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*)

Ivan Arismendi, Brooke E. Penaluna, and Stanley V. Gregory

Abstract Quantifying the dynamics of natural populations is a central issue in ecology. In the Pacific Northwest of North America, climate extremes are becoming more frequent and severe with projections of increasing winter floods and prolonged droughts during summer. Using a 13-year dataset of adult (Age 1+) Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*), we evaluated the effects of three droughts on annual growth and condition in two stream reaches of Mack Creek, H.J. Andrews Experimental Forest, Oregon, USA. In the three drought years, the onset of seasonal low flow consistently started earlier than reference water years and extended longer, from mid June until the end of September. We found consistent evidence of slower individual growth rates across sizes in drought years relative to reference years, with an apparent greater effect in larger trout. The median annual responses of trout were highly synchronous between stream reaches. There was evidence of slower growth and reduced condition associated with higher trout abundances in the two reaches. In addition, we found that growth rate and condition were associated with timing (annual maxima) and frequency (days >14 °C) of warm events, and habitat size (pool depth). Faster growth rates, higher abundance, and improved condition occurred in the second-growth forest reach compared to the old-growth forest reach. These results illustrated that a combination of density-dependent and density-independent processes can explain observed patterns in growth and condition over time. Each drought year had different climatic characteristics compared to reference years, including differences in the timing of precipitation, timing and magnitude of winter peak flows, and stream temperatures (especially in winter). Collectively, our findings suggest that growth and condition of adult trout

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are influenced by a complex interplay between density-dependence and density-independent factors. Thus, predictions about the effects of droughts on growth and condition in stream salmonids are difficult to generalize across regions. Our study highlights the value of long-term datasets because we can weigh the importance of processes that occur over both the short- and long-term.

Keywords Population regulation · Density-dependent · Density independent · Cascade Range · Environmental extremes · Refuges · Ecohydrology · Climate change

1 Introduction

The main mechanisms regulating growth in stream salmonids have been extensively discussed (reviews by Elliott 1994; Grossman and Simon 2020). Growth is predominantly regulated by density-dependent factors, even at low population densities (Grant and Imre 2005; Lobón-Cerviá 2007; Jenkins et al. 1999; Utz and Hartman 2009; Grossman and Simon 2020) owing to competition for food and space (Chapman 1966). Density-dependence can decrease resource availability per capita resulting in reduced individual fitness (e.g., growth). However, understanding the role of density independence in the regulation of population of stream salmonids is of great relevance given that droughts are expected to increase in frequency, magnitude, and duration (Huntington 2006; Vörösmarty et al. 2010; Trenberth 2011).

Drought affects species and their environments including habitats, water quality (e.g., temperature, fine sediments), food abundance, and predation (Lake 2003; Magoulick and Kobza 2003; Walters 2016; Lennox et al. 2019). All of these are central components influencing the growth regimes of fishes (Armstrong et al. 2021). Drought, defined as "significant low-flow periods" (Humphries and Baldwin 2003; Garner et al. 2015), reduces the size and diversity of riverine habitats and decreases pool connectivity (Lake 2003; Hakala and Hartman 2004; Kaylor et al. 2019; Lennox et al. 2019). Extreme high temperatures and low dissolved oxygen concentrations can also occur more frequently during drought (Lake 2003; Magoulick and Kobza 2003). In addition, site-specific changes in invertebrate densities (Cowx et al. 1984; Lake 2003; Bogan et al. 2015; Piniewski et al. 2017) and drift (Harvey et al. 2006; Wooster et al. 2016; González et al. 2018) have been observed during extreme low-flow periods. Some habitats can operate as temporal drought refuges (Keppel et al. 2012), concentrating resources and likely increasing species interactions (Dunham and Vinyard 1997; Humphries and Baldwin 2003; Lake 2003; Magoulick and Kobza 2003; Lennox et al. 2019). However, drought and its effects are often idiosyncratic owing to differing frequency, magnitude, and duration (Garner et al. 2015), as well as the condition of the ecosystems (Lake 2003; Magoulick and Kobza 2003; Walters 2016; Lennox et al. 2019). The recognition of

this idiosyncrasy can help improve the assessment and forecasting of the vulnerability of species and ecosystems (Walters 2016). To date, studies about the responses of stream salmonids to drought are scarce and often short term, <5 years (Walters 2016; Piniewski et al. 2017; Lennox et al. 2019; Kaylor et al. 2019).

Fishes that are adapted to regular seasonal low flow seem to recover rapidly after drought (Humphries and Baldwin 2003; Piniewski et al. 2017; Kaylor et al. 2019). Stream salmonids in areas with connected habitats can move (Milner et al. 1978; Mann et al. 1989; Gowan et al. 1994; Gresswell and Hendricks 2007) and likely seek out temporal drought refuges (Klemetsen et al. 2003; Magoulick and Kobza 2003; Sotiropoulos et al. 2006). Population responses of stream salmonids to drought seem relatively consistent, including a short-term reduction in abundance (Elliott 1984; Hakala and Hartman 2004; Kaylor et al. 2019), biomass (Sotiropoulos et al. 2006; James et al. 2010; Kaylor et al. 2019), or recruitment (Cowx et al. 1984; Titus and Mosegaard 1992; Lobón-Cerviá 2009; Elliott 2015; Blum et al. 2018). Less is known about the growth and condition of stream salmonids in response to drought. Growth seems to be reduced on both seasonal (Harvey et al. 2006; Nuhfer et al. 2017) and annual (Elliott 1984; Weatherley et al. 1991) bases during drought. Interestingly, potential compensatory growth responses (Ali et al. 2003) can emerge after consecutive summer droughts (Elliott 2015). Body condition of stream salmonids appears to be less consistent in whether there is a response to drought. For example, in one case, a significant reduction in condition was observed, suggesting limited food resources (Hakala and Hartman 2004). In other cases, no apparent changes in condition occurred during drought compared to reference years (Weatherley et al. 1991; James et al. 2010; Kaylor et al. 2019). Important questions remain about the relationship of individual growth variability by size or age as well as long-term patterns of growth between droughts and regular seasonal low-flow periods. Understanding these relationships between trout and flow is relevant to establish a baseline for species and ecosystems under climate change.

Here, we use 13 years of data (2008–2019), including three drought years, to characterize patterns of growth in adult Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) near the headwaters of Mack Creek, Oregon. Drought disproportionately affects headwater locations relative to downstream areas (Lake 2003; Nuhfer et al. 2017; Olson and Burton 2019) and large rivers appear to be more drought tolerant than small rivers (Lennox et al. 2019). Consequently, small, headwater streams are the ideal study system to understand the effects of drought. We assess the influence of drought on individual annual growth rate and condition of trout collected at the end of the low-flow period each year. We use concurrent information to describe density-dependent (trout abundance) and density-independent (temperature, flow, and habitat size) factors influencing the observed growth and condition of trout over time.

Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) populations are widely distributed from Alaska to California (Behnke 1992; Penaluna et al. 2016a). They are a tertiary consumer that numerically dominates headwater streams in the Pacific Northwest of North America (Hawkins et al. 1983). For stream-living trout, their lifespan is often 4–5 years, but can be up to 7–8 years. Individuals mature at age 2

and their home range is generally restricted to within 200 m of their birthplace (Trotter 1989).

Seasonal low flow is associated with lower survival of Coastal Cutthroat Trout (Berger and Gresswell 2009; Sheldon and Richardson 2021), and the ability of this species to move in headwaters is more restricted than in downstream areas (Trotter 1989; Gresswell and Hendricks 2007). Most behaviors of Coastal Cutthroat Trout are responses to cope with the perceived threat of predation (Harvey and Nakamoto 2013; Penaluna et al. 2016b; Penaluna et al. 2021), such as grouping, habitat shifting, and lack of feeding (Penaluna et al. 2021), which would be more energetically costly during drought. Energy expenditure is exacerbated as warmer temperatures increase trout metabolism (Dwyer and Kramer 1975) and drought refuges will likely support higher trout densities, leading to more intraspecific competition (Dunham and Vinyard 1997; Penaluna et al. 2021) and slower growth rates. Eventually, these extreme circumstances could lead to mortality or migration to other habitats, resulting in lower densities at the end of the drought. We hypothesize that slower growth and reduced condition of adult trout will occur during drought relative to reference years because of increased energy expenditure and competition for food resources. Collectively, our findings show that long-term studies provide foundational information for answering complex questions that emerge from climate change and support the conservation of stream salmonids.

2 Methods

2.1 Study Sites and Historical Context

The study sites (Fig. 1) were two stream reaches in Mack Creek (old-growth and second-growth; 580 ha), which is part of the H.J. Andrews Experimental Forest in the Willamette National Forest and is protected for research purposes (Swanson et al. 1982). The old-growth stream reach flows through a dense old-growth conifer forest dominated by ancient Douglas-fir (*Pseudotsuga menziesii*) up to 700 years old (Gregory et al. 1991). The second-growth stream reach was clearcut in 1964 (46 years before the start of our study in 2008; Gregory et al. 1991). Physical legacy effects of forest harvest are expected to be minimal after 20 years (Jones and Post 2004; Mellina and Hinch 2009; Moore and Wondzell 2005; Penaluna et al. 2015).

2.2 Animal Collection and Tagging

Each captured trout was measured to fork length (FL; 1.0 mm) and mass (1.0 g). In each stream reach, we sampled trout from the same three contiguous 50-m sections (150 m total) during the first week of September every year. We used a standard

Fig. 1 Our study sites, including second- and old-growth reaches in Mack Creek, H.J. Andrews Experimental Forest, Oregon

electrofishing procedure with block nets for each 50-m section. Abundance was estimated using the two-pass depletion method (Seber and Le Cren 1967); sampling was limited to two passes to minimize negative impacts on fish. Probability of capture exceeded 0.7 in all reaches; two-pass depletion is considered unbiased if probability of capture exceeds 0.2 (Stewart et al. 2019). All trout FL ≥ 60 mm were implanted with a 12-mm full-duplex passive integrated transponder (PIT tag;

Oregon RFID, Portland, Oregon) in the ventral body cavity using a syringe sterilized in 90% ethanol.

In our analysis, we focused on recaptured adult trout (Age 1+; FL > 70 mm). We estimated the relative annual growth rate (RGR, Ricker 1975) from the previous year to the time of capture as $RGR = [(L_i - L_{i-1})/L_{i-1}] \times 100$ where L_i is the length at the time of capture and L_{i-1} is the length from the previous year. In addition, we calculated Fulton's condition factor (Ricker 1975) as a measure of the well-being of fishes (Blackwell et al. 2000; Froese 2006). Fulton's condition factor was calculated as $K = (M_i/L_i^3) \times 100{,}000$ where M_i and L_i were the observed individual mass (g) and length (mm) at the time of recapture.

We tagged 3695 trout in the two reaches (54% at the second-growth reach; 46% at the old-growth reach) between 2008 and 2019. The percent of recaptured trout per year relative to the number of tagged trout in the previous year was comparable between reaches (second-growth: median = 26%, range = 21–32%; old-growth: median = 28%, range = 22–41%). The median number of recaptured trout across years was 41 in the two-stream reaches and fluctuated between 36 (2010) and 55 (2015) in the second-growth reach, and between 31 (2013) and 57 (2012) in the old-growth reach. There was no association in the number of recaptured trout between reaches over time (Pearson Product Moment Correlation $r = 0.48$, $P = 0.213$).

2.3 Environmental Datasets

We extracted daily hydrometeorological information from existing datasets available at the H.J. Andrews Experimental Forest. These data were air temperature and precipitation (Daly et al. 2019), daily streamflow (Johnson et al. 2020), stream temperature (Gregory and Johnson 2019), and geometry of pool habitats (Gregory and Arismendi 2020). Specifically, we selected three sentinel pools representing essential trout habitat during seasonal low flow in each stream reach. We used the same three pools per reach each year. We used maximum pool depth and calculated the pool area (A) as an ellipse (i.e., $A = \pi \times a \times b$, where a is the max length and b is the max width of the respective pool).

We defined drought as a "significant low-flow period" (Humphries and Baldwin 2003) within the water year (WY; from October 1 to September 30). The low-flow period in our study system extended from June 15 to September 30, we classified Water Years 2015, 2018, and 2019 as drought years as they had both lowest and longer low-flow periods in our study. In addition, 2015 and 2018 were classified regionally as drought years (https://www.drought.gov/states/oregon/county/lane).

2.4 Statistical Analyses

Because limits on annual growth rates related to size can be affected by multiple limiting factors (e.g., age, food, temperature, and metabolism), we adopted a quantile regression approach (Cade and Noon 2003) to model growth rate in drought versus reference years. We fitted multiple quantile regression models between individual size and annual growth rate of recaptured trout ($n = 849$) using the "quantreg" package (Koenker et al. 2018) in *R* (Version 3.6.0).

We tested difference in median growth rate of trout among years (2009–2019) using a Kruskal-Wallis ANOVA on ranks. We adopted this test because our somatic data were not normally distributed. In addition, we used Dunn's method as pairwise multiple comparisons to identify years that differed from the others. We conducted a similar procedure to test differences in condition (K), and size of recaptured trout over the years. We tested for potential differences in trout abundance between the two stream reaches during our study period using Student's t-test.

We performed simple Pearson product moment correlation analyses to explore potential coherence between reaches in the association of annual metrics of trout (i.e., growth and condition) and relevant covariates representing density-dependent (adult trout abundance) and density-independent environmental factors (streamflow, stream temperature, and habitat size). We used several metrics of flow and temperature to account for seasonality of the stream environments (magnitude, variability, and timing) and their relevance for stream salmonids in this region (Arismendi et al. 2013; Olden and Poff 2003). For streamflow, we included annual minimum, maximum, as well as mean, and standard deviation during relevant periods (winter: Jan–Feb; spring: Mar–May, summer: Jul–Aug). For stream temperature, we included annual minimum and maximum, mean and standard deviation of relevant period (winter, spring, and summer), timing of the annual max, and frequency of days >14°C and < 16°C (peak growth of *O. clarkii* is 13.6°C and 16°C based on a fitted curve and measured empirically based on Bear et al. 2007, respectively). For habitat size, we included the mean maximum depth and area of sentinel pools. Lastly, we used simple Pearson product moment correlation analyses to test the synchrony of median annual metrics of trout (growth, condition, size, and abundance) between stream reaches. All statistical analyses were performed using the software R ver. 3.6.0.

3 Results

3.1 *Growth and Condition of Adult Trout Between Drought and Regular Seasonal Low Flow*

Individual annual relative growth rates of adult trout (mm/year) varied across size, ranging from 1.5 to 43% with higher variability in smaller compared to larger trout (Fig. 2). This pattern was consistent between the two stream reaches over the study

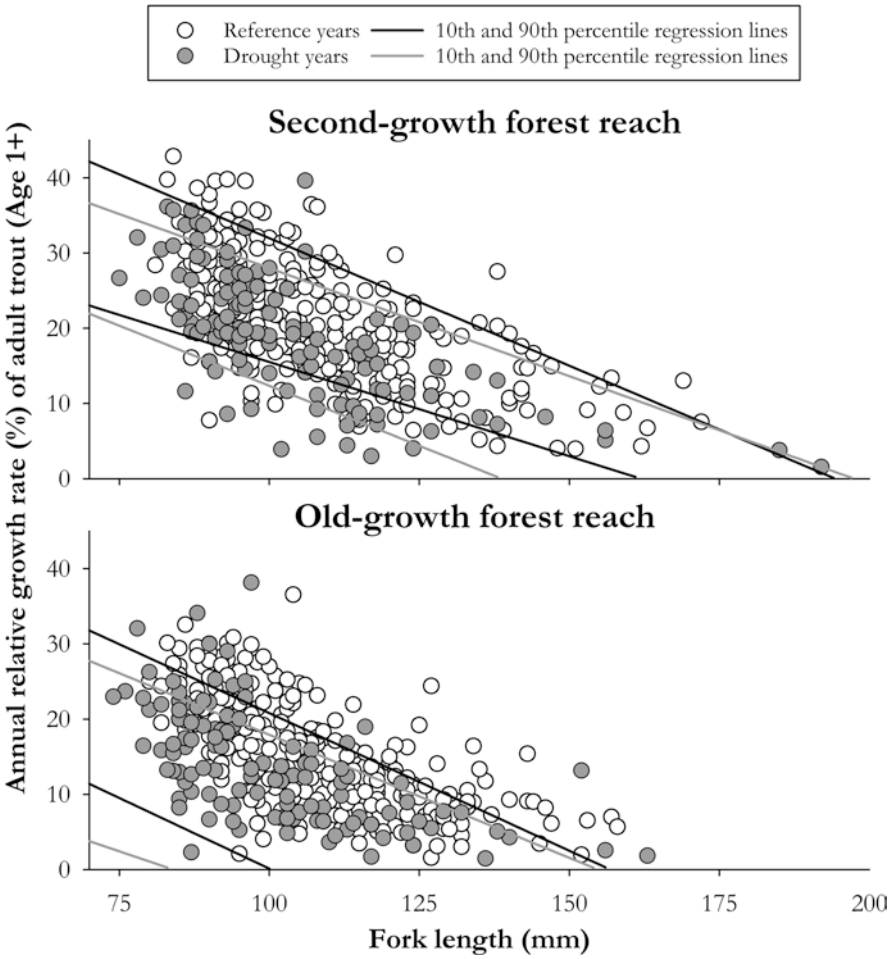

Fig. 2 Annual relative growth rate of individual adult trout (%) by size (mm) during reference (open circles; 2009–2014, and 2016–2017) and drought (gray circles; 2015, 2018–2019) years in the two reaches of Mack Creek in H.J. Andrews Experimental Forest, Oregon. Lines represent 10th and 90th quantile regressions curves for each second-growth (gray lines) and old-growth (black lines) reaches

period. Upper quantile regression lines (90th percentile) representing the maximum scope of growth of adult trout by size illustrated overall slower growth rates during water years of droughts compared to reference water years (hereafter referred to as drought years and reference years). The slope of the regressions across all quantiles (Tau in Fig. 3) appeared to be relatively similar between reaches during reference years. However, negative slopes tended to be more pronounced during drought in larger trout (upper quantiles), illustrating a potentially limited scope of growth for this size group. Consistently, there were statistically significant differences ($P < 0.001$) in the median growth rate of trout between drought and reference years

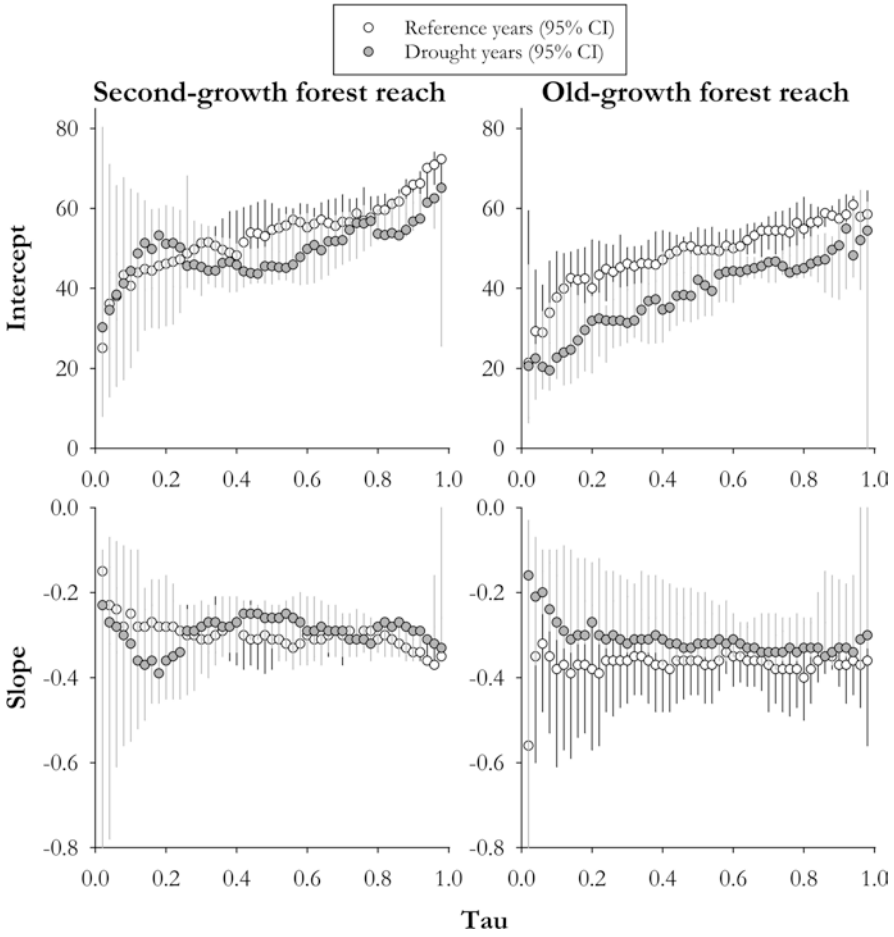

Fig. 3 Slopes and intercepts of multiple quantile (Tau) regression curves representing the scope of growth of adult trout across sizes during reference (2009–2014 and 2016–2017) and drought (2015 and 2018–2019) years in two stream reaches in Mack Creek, Oregon. Larger trout are represented by upper quantiles whereas smaller trout are represented by lower quantiles

in the two reaches (Fig. 4); adult trout had slower growth rates in drought years compared to reference years.

Median annual relative growth rates (%) of adult trout also fluctuated over time (Fig. 4), but they were highly synchronous between reaches ($r = 0.79$; $P = 0.003$). The slowest relative growth rates occurred during two of the three drought years (2015 and 2019), but also during some reference years (2012 in the old-growth

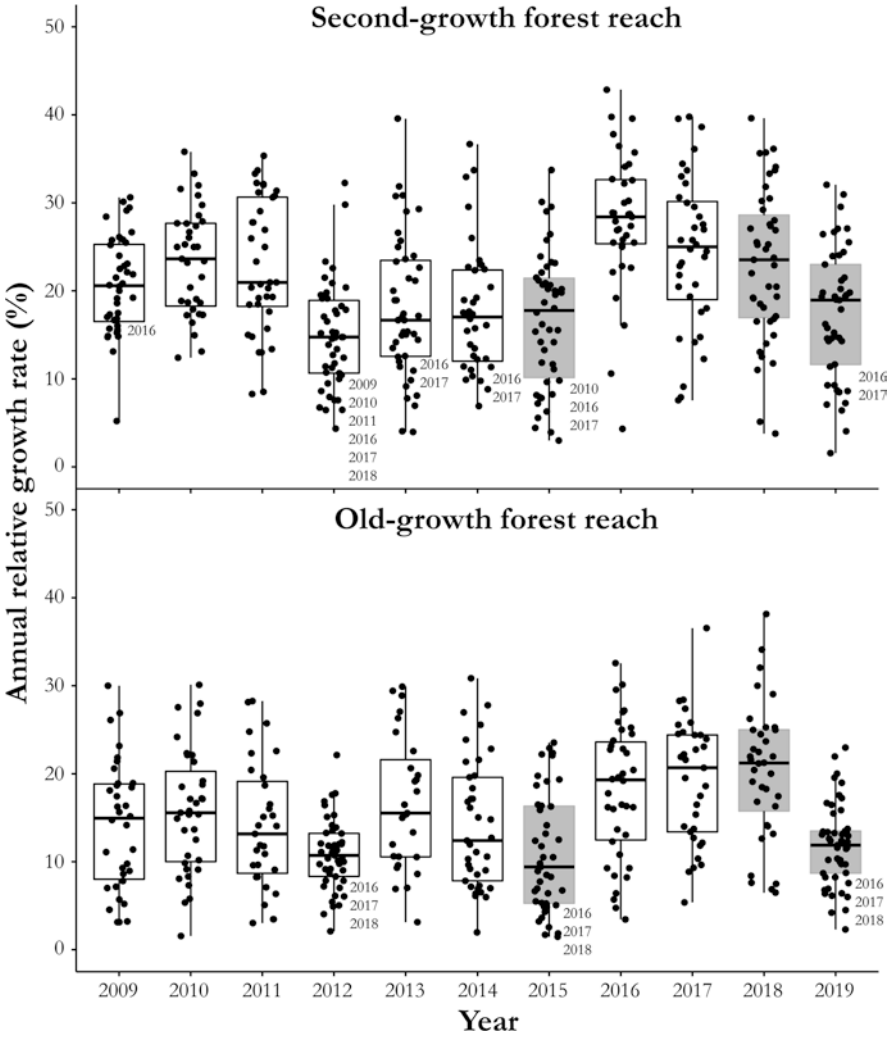

Fig. 4 Annual relative growth rate (%) of recaptured trout in two reaches of Mack Creek, Oregon. Gray boxes indicate drought years. Kruskal-Wallis one-way ANOVA on ranks showed significant differences among years (second-growth reach: H = 92.96, df = 10, $P < 0.001$; old-growth reach: H = 70.070, df = 10, $P < 0.001$). Numbers adjacent to boxes identify years with significant differences from pairwise comparisons (Dunn's Method $P < 0.05$)

reach, and 2012–2014 in the second-growth reach). Overall, relative growth rates were greater in the second-growth reach (median of 20.6%) compared to the old-growth reach (median of 14.9%). However, most abrupt differences among years were observed in the second-growth reach as illustrated by markedly low growth during 2012–2015.

Median condition of recaptured adult trout was relatively high (Fulton's condition >1.3) across years with notable annual fluctuations (Fig. 5), and relatively high synchrony between reaches (r = 0.79; P = 0.004). The median condition of trout across years was higher in the second-growth reach (median of 1.71) compared to the old-growth reach (median of 1.56). Yet, the largest differences in condition were observed in the second-growth reach as seen during 2012–2015. Interestingly, the two lowest condition values of trout did not occur during a drought year (2012 or 2014) in the second-growth reach. In the old-growth reach, the highest condition score occurred during a drought year (2018), whereas the lowest median condition score occurred in the drought year 2015 and the second lowest score in the reference year 2012. Median annual Fulton's condition and median annual growth rate of adult trout were strongly associated in both reaches (second-growth reach: $r = 0.96$, $P < 0.001$; old-growth reach: $r = 0.90$, $P < 0.001$).

Given growth rates were inversely related to trout size (Figs. 1 and 2), changes in size over time could influence year-to-year growth rate estimates. Median size (FL) of recaptured adult trout (Fig. 6) was synchronous between reaches (r = 0.58; $P = 0.047$). In the second-growth reach, recaptured trout had a median size of 102.5 mm, ranging between 96 (2016, 2019) and 115 mm (2012). In the old-growth reach, the median size of recaptured trout was comparable to the second-growth reach (104 mm, ranging between 91 in 2018 and 113 mm in 2013). Recaptured trout in the old-growth reach were smaller ($P < 0.05$) in 2018 and 2019 compared to reference years. In the second-growth reach, recaptured trout were larger in 2012 compared to 2015–2016 and 2018–2019.

3.2 Density-Dependence Affecting Growth and Condition of Adult Trout

There were two distinct periods of relatively high (2009–2014) and low (2015–2019) adult trout abundances (Fig. 7) with a high synchrony between the two reaches ($r = 0.82$; $P = 0.002$). Overall, the mean (± SD) abundance of adult trout was slightly higher in the second-growth reach (70 ± 12 ind./50 linear m) compared to the old-growth reach (60 ± 7 ind./50 linear m). In the second-growth reach, highest abundance occurred in 2010, 2012, and 2014, whereas the lowest occurred in 2016. In the old-growth reach, the highest and lowest trout abundance occurred in 2014 and 2016, respectively. Moreover, there was a consistent negative association between annual trout abundance and growth rate in both reaches, especially in the second-growth reach (Table 1). Similarly, there was a negative association between annual

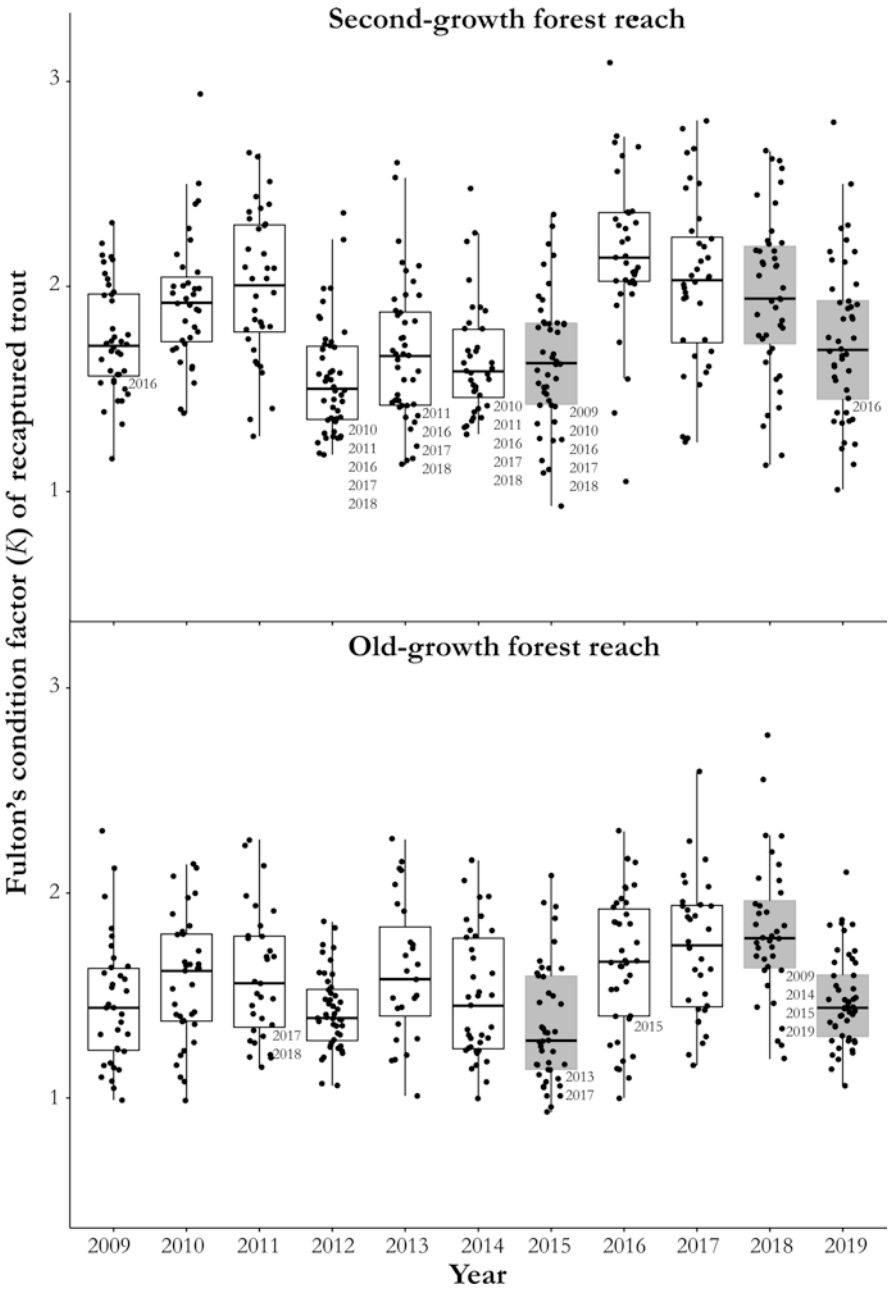

Fig. 5 Fulton's condition factor (*K*) of recaptured trout in the two reaches of Mack Creek, Oregon. Gray boxes indicate drought years. Kruskal-Wallis one-way ANOVA on ranks showed significant differences among years (Second-growth reach: $H = 106.58$, df = 10, $P < 0.001$; Old-growth reach: H = 64.30, df = 10, $P < 0.001$). Numbers next to the boxes identify years with significant differences from pairwise comparisons (Dunn's Method $P < 0.05$)

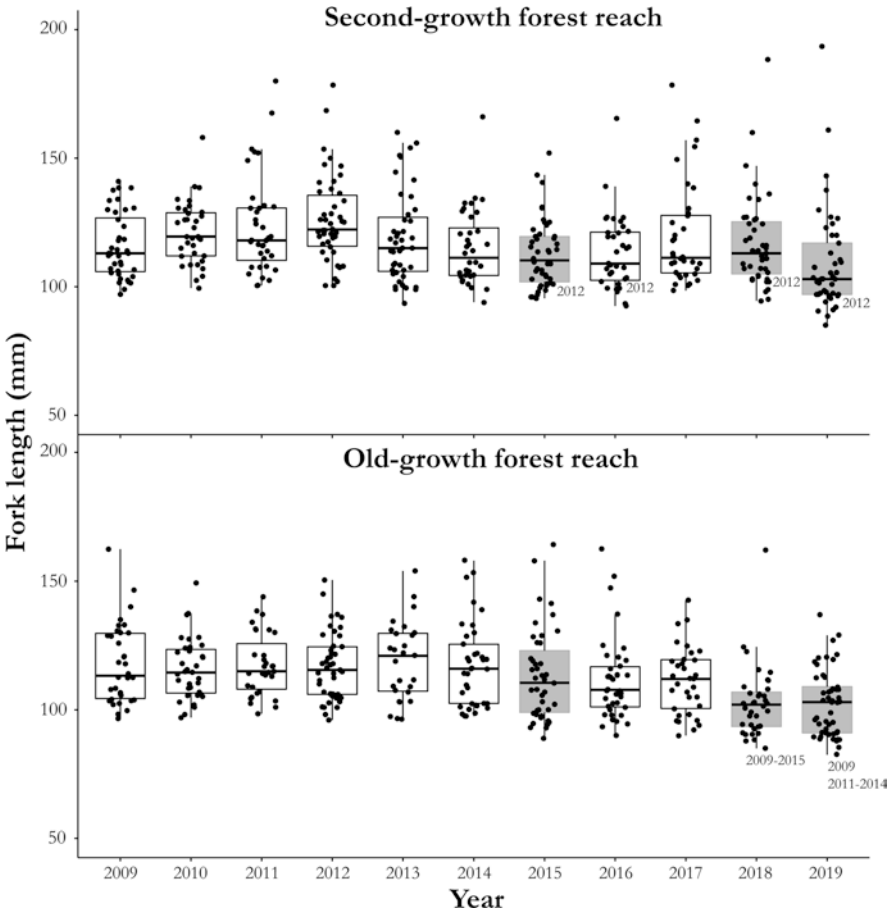

Fig. 6 Recaptured trout sizes in two reaches from Mack Creek, Oregon. Gray boxes indicate drought years. Kruskal-Wallis one-way ANOVA on ranks showed significant differences among years (Second-growth reach: H = 40.97, df = 10, $P < 0.001$; Old-growth reach: H = 60.87, df = 10, $P < 0.001$). Numbers next to the boxes identify years with significant differences from pairwise comparisons (Dunn's Method $P < 0.05$)

trout abundance and condition in both reaches that was marginally significant in the second-growth reach ($r = -0.53$; $P = 0.092$).

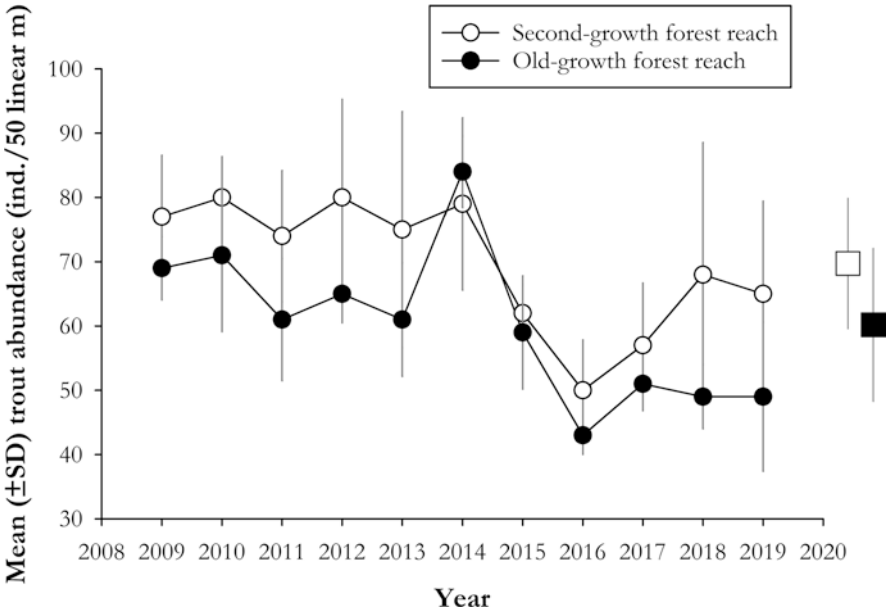

Fig. 7 Adult trout (Age 1+) abundance (mean ± SD) between 2009 and 2019 in two reaches in Mack Creek, Oregon. Square symbols at the right side of the graph show mean ± SD trout abundance for the entire study period. The difference in the mean trout abundance between the two stream reaches was marginally significant (Student's *t*-test $t = 2.023$, df = 20, $P = 0.057$)

3.3 Density-Independence Affecting Growth and Condition of Adult Trout

As is expected for a typical Mediterranean-climate region (hot-dry summers and cool-wet winters), the hydroclimate for the Mack Creek basin was influenced by a strong seasonality in precipitation, streamflow, and air/stream temperature (Figs. 8 and 9). Drought years (2015, 2018, and 2019) received approximately 21% less annual precipitation in summer and early autumn compared to reference years (2009–2014 and 2016–2017). Differences in hydroclimate were notable among drought years, with 2015 as the most extreme. In 2015 and 2018, a greater proportion of the precipitation (71% and 74%, respectively) occurred before the end of February compared to 2019 (61%) or the reference years (average of 59%; Fig. 8). Winter peak flows in 2015 and 2018 were also lower than during reference years. In 2019, there was an unusually high-flow event in April. In all drought years, the onset of the low-flow period started earlier, around mid June, and extended later until the end of September compared to reference years.

There was a consistent negative association between annual daily maximum streamflow and growth rate in both reaches ($r > |0.42|$; Table 1), but this relationship was not statistically significant. Relatively similar findings occurred for condition of trout in both reaches ($r > |0.36|$). Other metrics accounting for the magnitude and

Table 1 Pearson product moment correlation analyses between median annual responses of trout (growth rate and condition) and density-dependent and density-independent factors during 2009–2019 in two reaches (second-growth, and old-growth) of Mack Creek, H.J. Andrews Experimental Forest, Oregon. Significant values ($P < 0.05$) in bold and marginally significant ($P < 0.1$) in italics

	Annual relative growth rate (%)				Condition (Fulton's K)			
	Second-growth		Old-growth		Second-growth		Old-growth	
Metric	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value
Density-dependent factors								
Mean adult trout abundance (ind./50 linear m)	−0.63	**0.039**	−0.49	0.131	−0.53	*0.092*	−0.40	0.219
Density-independent factors								
Streamflow								
Annual daily maximum streamflow (m^3/s)	−0.42	0.202	−0.49	0.125	−0.36	0.278	−0.51	0.108
Mean winter streamflow (Jan–Feb; m^3/s)	−0.10	0.779	−0.06	0.860	−0.12	0.717	−0.12	0.732
SD of winter streamflow (Jan–Feb; m^3/s)	−0.24	0.484	−0.27	0.425	−0.13	0.700	−0.23	0.497
Mean spring streamflow (Mar–May; m^3/s)	0.00	0.994	0.18	0.604	0.09	0.801	0.22	0.519
SD of spring streamflow (Mar–May; m^3/s)	−0.15	0.664	−0.10	0.770	−0.16	0.633	−0.08	0.805
Annual daily minimum streamflow (m^3/s)	−0.23	0.494	−0.13	0.694	−0.06	0.854	−0.08	0.820
Mean summer streamflow (Jul–Aug; m^3/s)	−0.19	0.574	−0.24	0.469	0.01	0.973	−0.02	0.955
SD of summer streamflow (Jul–Aug; m^3/s)	−0.22	0.513	−0.27	0.421	−0.01	0.966	−0.06	0.866
Stream temperature								
Annual daily minimum stream temperature (°C)	−0.18	0.610	−0.30	0.401	−0.19	0.601	−0.33	0.357
Mean winter stream temperature (Jan–Feb; °C)	0.17	0.638	−0.21	0.554	0.10	0.778	−0.24	0.514
SD of winter stream temperature (Jan–Feb; °C)	0.09	0.798	0.01	0.972	0.04	0.906	0.05	0.887
Mean spring stream temperature (Mar–May; °C)	0.12	0.747	−0.07	0.851	0.10	0.789	−0.13	0.729
SD of spring stream temperature (Mar–May; °C)	−0.02	0.949	0.13	0.727	−0.03	0.938	0.05	0.891
Annual daily maximum stream temperature (°C)	−0.26	0.439	−0.21	0.536	−0.44	0.175	−0.40	0.224
Timing of annual temperature max (ODWY)	0.26	0.478	0.41	0.239	0.43	0.211	0.58	*0.077*
Mean summer stream temperature (Jul-Aug; °C)	−0.32	0.344	−0.03	0.928	−0.34	0.303	−0.17	0.626

(continued)

Table 1 (continued)

	Annual relative growth rate (%)				Condition (Fulton's K)			
	Second-growth		Old-growth		Second-growth		Old-growth	
SD of summer stream temperature (Jul-Aug; °C)	0.09	0.798	0.01	0.972	−0.03	0.922	−0.07	0.834
Number of days >14 °C	−0.21	0.565	−0.39	0.265	−0.34	0.341	−0.56	*0.095*
Habitat size								
Mean maximum depth of sentinel pools (m)	0.17	0.613	−0.54	*0.084*	0.24	0.473	−0.55	*0.079*
Mean area of sentinel pools (m^2)	−0.44	0.180	0.37	0.270	−0.30	0.365	0.32	0.334

variability of seasonal streamflow did not show clear associations with either growth or condition of adult trout.

Thermal regimes in the Mack Creek basin differed among drought years (Fig. 9). The winter (January–February) of 2015 was 4.0°C warmer than the average of winters in reference years, but only 1.2°C warmer in 2018–2019. Similarly, the summer (July–August) of 2015 was 1.65°C warmer than the average of summers in reference years, but only 0.68°C warmer in 2018–2019. Water temperature conditions (7-day moving average) of Mack Creek were relatively cold, ranging between 0.9°C and 13.6°C. Summer stream temperatures in drought years were not the warmest in our study period, except for an early peak in late June of 2015. During this drought year, the average winter stream temperature was 1.9°C warmer than the average in reference-year winters.

There was a consistent positive association between timing of annual daily maximum temperature and growth rate in both reaches ($r > 0.26$, Table 1), but this association was not statistically significant. A similar finding occurred for condition of adult trout ($r > 0.43$; it was marginally significant in the old-growth reach). Later timing of maximum temperature was associated with faster growth and greater condition of trout. These associations were marginally significant in the old-growth reach ($r > 0.57$). In addition, there was a consistent negative association between the number of days exceeding 14°C and growth rate in both reaches ($r > |0.26|$) with similar patterns occurring for condition ($r > |0.43|$). The association was marginally significant in the old-growth reach for condition ($r = -0.58$). Similarly, there was a consistent negative association between annual daily maximum temperature and both growth and condition ($r > |0.21|$ and $r > |0.4|$, respectively, Table 1), but these associations were not statistically significant. Other metrics (Table 1) accounting for the magnitude and variability of seasonal stream temperature did not show clear associations with either growth or condition of trout.

Pool geometry from late summer (early September) was used as a proxy of trout habitat conditions during seasonal low flow for each water year. Sentinel pools showed relatively similar geometry during our study period (Fig. 10). Mean maximum pool depth across years was similar between reaches (0.56 m), whereas the pool area was 8% smaller in the second-growth compared to the old-growth reach. Mean annual maximum pool depth was deeper in both second-growth (21%) and

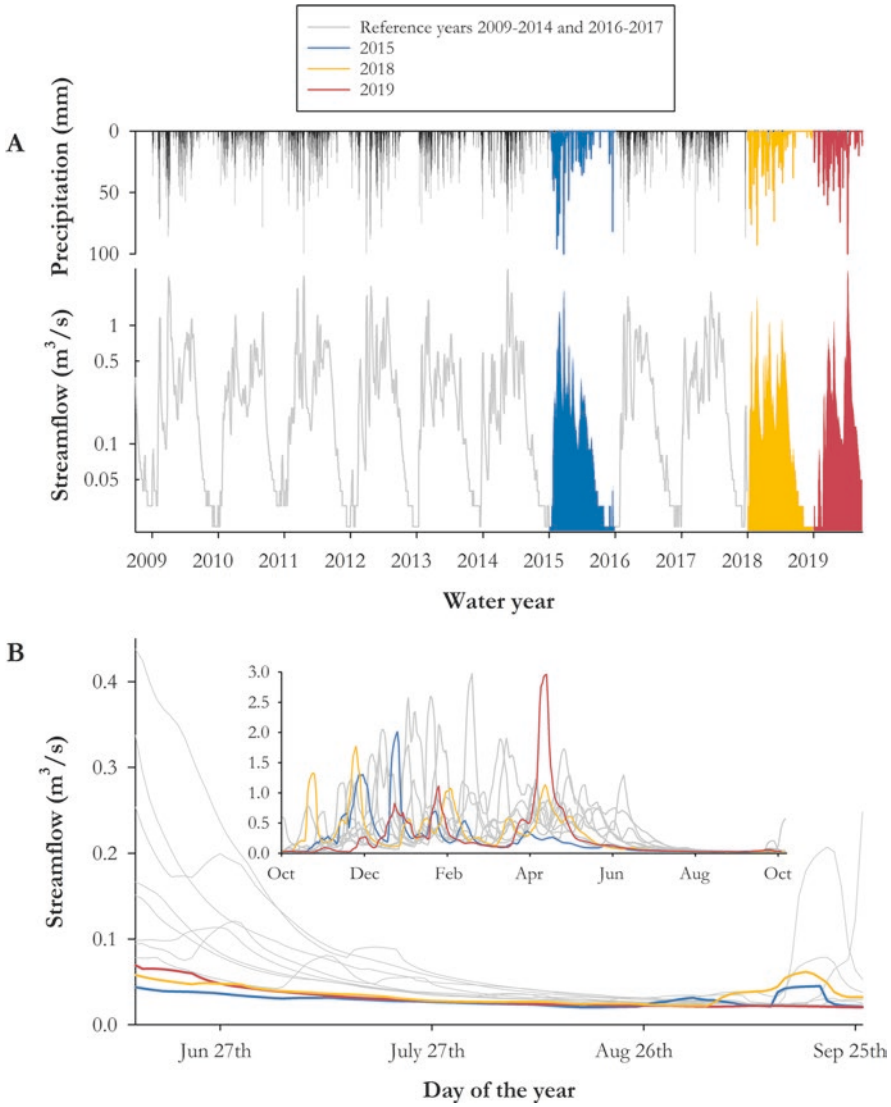

Fig. 8 (**a**) Time series (WY 2009–2019) of precipitation (mm) and streamflow (m^3/s) in Mack Creek, Oregon. Water years were classified as reference (2009–2014 and 2016–2017) or drought years (2015, 2018, and 2019). Total daily precipitation data (available up to March 18, 2019) were extracted from the UPLMET station (Daly et al. 2019) and presented as daily values. Daily mean streamflow data were extracted from the GSWSMC gauge station (Johnson et al. 2020) and presented as 7-day moving average values. (**b**) Zoom-in to the seasonal low-flow period and annual streamflow (inset) across years

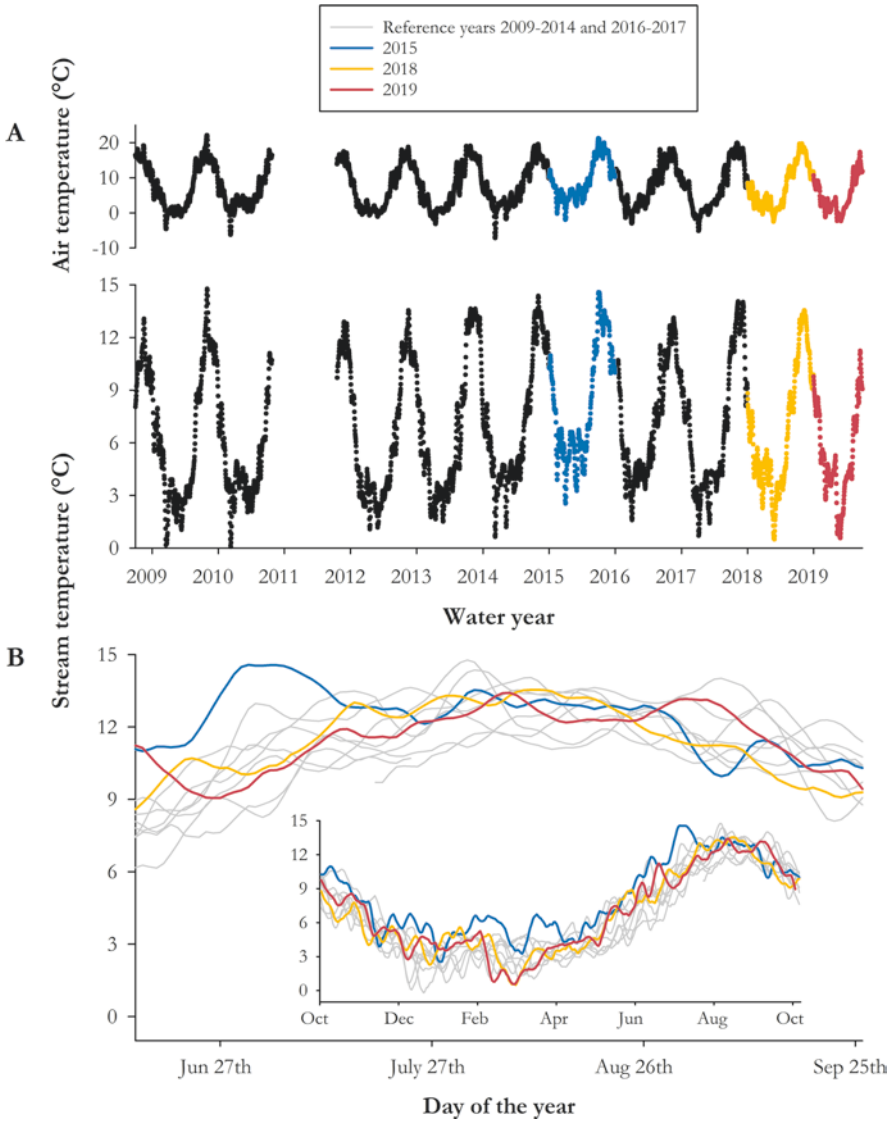

Fig. 9 (**a**) Time series (WY 2009–2019) of air and stream temperature (°C) for Mack Creek, Oregon. Water years were classified as reference (2009–2014 and 2016–2017) and drought years (2015, 2018, and 2019). Mean daily stream and air temperature data were extracted from the GSMACK and TSMACK stations (Gregory and Johnson 2019) and presented as 7-day moving average values. Small gaps (<30 days) in air temperature data were filled using a simple linear regression between GSMACK vs TSMACK ($y = 1.024x–0.29$; $R^2 = 0.95$). Small gaps (<30 days) in stream temperature data were filled using a simple linear regression between GSMACK vs TSMACK ($y = 1.01x–0.79$; $R^2 = 0.95$). (**b**) Zoom-in to seasonal low-flow period and annual temperature regime (inset) across water years

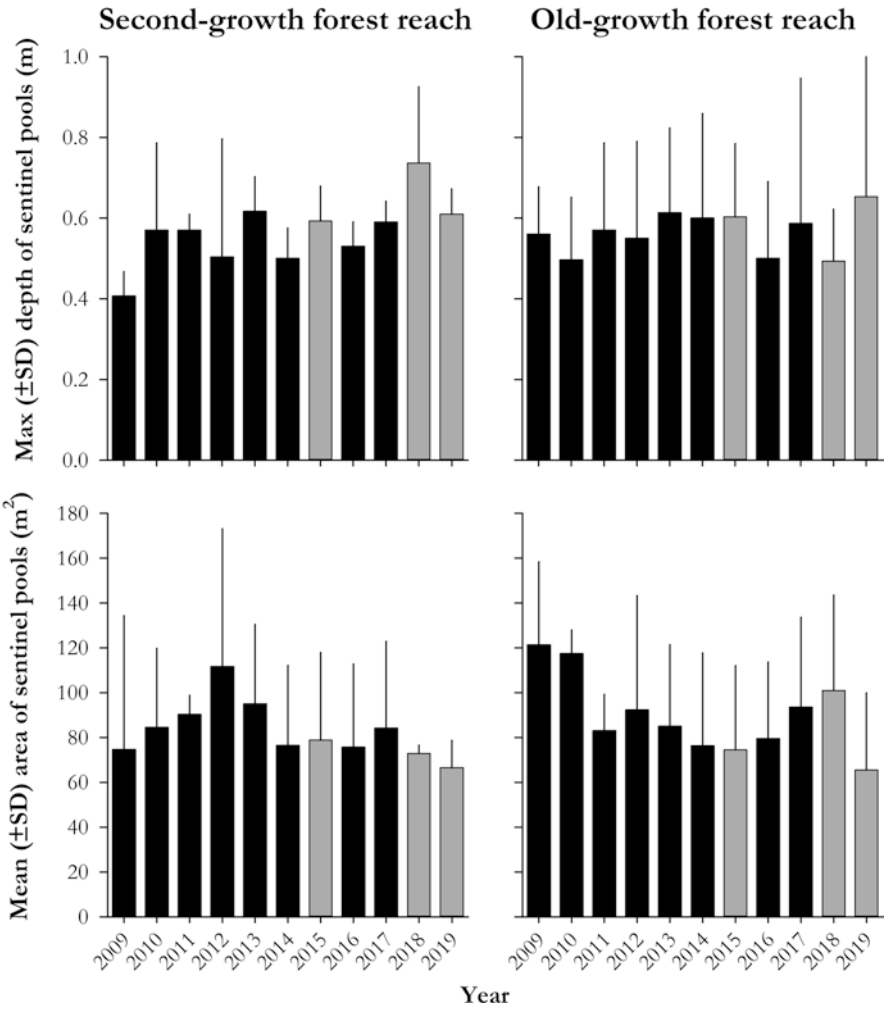

Fig. 10 Time series (WY 2009–2019) of the geometry of sentinel pools ($n = 3$) surveyed at the end of the summer in the two reaches from Mack Creek, Oregon. Gray bars indicate drought years

old-growth (4%) reaches during drought compared to reference years. However, mean annual pool area was consistently smaller in both the second- (26%) and old-growth (24%) reaches during drought relative to reference years. In particular, the drought in 2019 had the lowest pool area of all years at the two reaches.

There was a negative and marginally significant association between maximum pool depth and growth rate and condition of adult trout only in the old-growth reach ($r > |0.54|$, Table 1). This association was positive in the second-growth forest. Pool area did not show clear associations with either growth or condition of trout.

4 Discussion

Revealing the complex interplay between density-dependent and density-independent as regulators of growth in stream salmonids is essential for the conservation of species and ecosystems, especially given climate change. We demonstrated that there is low annual growth of individual adult trout (Age 1+) across size in drought years compared to reference years. The negative associations between growth or condition and abundance over time suggest density-dependence is a factor regulating the demography of trout populations in our study system. However, observed lower growth rates and reduced condition associated with years with higher annual peak flows, earlier timing of annual maximum stream temperature, and higher frequency of warmer days (>14°C) also are indications of density-independent effects. Collectively, our findings support both density-dependent and density-independent factors modulating growth and condition of adult trout, which has also been suggested in other studies (e.g., Elliott 2015; Uthe et al. 2019; Huntsman et al. 2021).

Density-dependent effects on growth seem to prevail under regular seasonal low flow, whereas density-independent factors become more relevant during droughts, similar to Power et al. (2008). Both annual growth rate and condition are negatively associated with abundance in our stream reaches across years. Yet, the logistic regression analysis revealed that (1) the variability of individual growth rates is greater in small compared to large individuals, suggesting that factors other than size can limit growth (see other examples in Cade and Noon 2003), and most importantly (2) the maximum scope of growth across sizes is reduced during drought compared to regular seasonal low-flow periods. A possible explanation for these findings is habitat segregation as a response to intraspecific competition during regular seasonal low flow (Chapman 1966; Elliott 1994; Lobón-Cerviá 2007; Jenkins et al. 1999). In the first case, dominant larger size-at-age individuals select and use best-quality habitats, whereas smaller size-at-age subordinate individuals occupy less-suitable habitats (Chapman 1966; Penaluna et al. 2021). As individual growth rates are likely a function of habitat quality (e.g., Wilzbach et al. 1986), the observed variability in individual growth rates during regular seasonal low flow would be indicative of the diversity and quality of available habitats between our stream reaches. In the second case, the slower growth rates of larger compared to smaller individuals can be explained by the higher metabolic requirements of larger individuals during summer (Dwyer and Kramer 1975; Hughes and Grand 2000), for example, increased allocation of energy to gamete production as trout grow. However, intraspecific competition and metabolic costs likely increase in importance owing to harsher environments during drought compared to regular seasonal low-flow periods. Specifically, streamflow and space are more constrained and a greater number of animals are likely to occupy drought refuges resulting in higher interference competition (e.g., Dunham and Vinyard 1997). Smaller and less diverse habitats available during drought (Lake 2003; Hakala and Hartman 2004; Kaylor et al. 2019; Lennox et al. 2019) would then result in the observed lower variability

of individual growth rates. In addition, trout behavior, such as movement and interactions between individuals (Penaluna et al. 2021) are likely energetically more costly and could limit the maximum scope of growth, as seen in our logistic regression analysis. We show some evidence of growth limitation affecting larger trout more than smaller trout, as suggested in other systems during drought (Walters 2016). We suspect that density-dependent and density-independent processes likely lead to differential responses and explain the impacts of droughts in other stream settings.

The high synchrony of trout responses in our stream reaches suggests an overarching effect of climate on the regulation of growth and condition of trout and yet, local conditions of each stream reach can temper the effects of drought (e.g., Matthews 1998; Magoulick and Kobza 2003; Walters 2016). We found that growth and condition are negatively associated with deeper pools in the old-growth reach, but this relationship is positive in the second-growth reach. The longitudinal profile of the old-growth reach is dominated by large wood supporting steps up to 2.5 m high that create low-gradient upstream channel segments with finer streambed sediments, whereas the longitudinal profile of the second-growth reach is dominated by boulder steps and larger streambed sediments (Faustini and Jones 2003). Water depth during the low-flow period is similar between the two reaches, but deeper pools (>0.5 m) are more common in the old-growth than the second-growth reach (Faustini and Jones 2003). Because food availability can limit trout growth during seasonal low flow (Boss and Richardson 2002), differences in the quality of foraging habitats might affect our findings. For example, pool habitats differing in overhead shading can affect invertebrate drift densities and foraging efficiencies, resulting in slower trout growth rates (Wilzbach et al. 1986). In addition, terrestrial prey becomes more important in the diet of stream salmonids during seasonal low flow (Romero et al. 2005; Sweka and Hartman 2008) and differences in terrestrial food resources between stream reaches from riparian habitats (Naiman and Décamps 1997) might also influence our findings.

Our study had several limitations, especially considering the myriad of factors and processes affecting riparian ecosystems (Gregory et al. 1991) including climate stochasticity. For example, there is a lack of spatial and temporal replication of our stream settings and drought events that limits the use of more robust statistical analyses (e.g., generalized linear mixed models). However, most research evaluating the effects of drought in rivers are short-term opportunistic studies that, by nature, are unable to consider environmental stochasticity (Lake 2003; Magoulick and Kobza 2003; Walters 2016; Piniewski et al. 2017; Lennox et al. 2019). Our study considers two adjacent stream reaches during a 13-year period that included three droughts, with two of them as consecutive events. Droughts and their effects seem to be idiosyncratic (Lake 2003; Humphries and Baldwin 2003; Magoulick and Kobza 2003; Walters 2016; Lennox et al. 2019) and thus, the transferability of our findings across species and ecosystems is limited. We did not consider factors related to trout emigration (Penaluna et al. 2021) or the seasonality of growth regimes (Armstrong et al. 2021), but these may not be important influences on trout in Mack Creek (Trotter 1989; Gresswell and Hendricks 2007). We had relatively high annual recaptures

(21–41%). The timing of our sampling at the end of the seasonal low flow each year allowed us to acquire a reliable record of growth and condition of trout during a stressful and critical period for Coastal Cutthroat Trout (Berger and Gresswell 2009; Sheldon and Richardson 2021). In addition, we were not able to evaluate the availability of food sources and the quality of both foraging habitats and drought refugia (e.g., Millidene et al. 2006). The dynamics of drift (Naman et al. 2016) as well as prey subsidies from terrestrial systems (Baxter et al. 2005) are complex processes and additional research is needed to better understand the role of local conditions on the creation of foraging habitats that can potentially buffer effects of droughts and thus, affect the growth and condition of stream salmonids.

Idiosyncratic aspects of the hydroclimate during each drought coupled with the effects of trout abundance illustrate the complex link between density-dependent and density-independent processes that affect the growth and condition of trout. Although the seasonal low-flow period has consistently lower flows and is of longer duration in drought years, responses of trout are not always the same. Differences in timing of precipitation, magnitude of winter peak flows, seasonal temperatures, and size of habitats during drought years can affect abundance as well as growth and condition of trout. The drought in 2015 represented the most extreme low-flow season of our study period, including the warmest winter and summer. Trout abundance was lower than in the previous years, but growth rate and condition were among the lowest in our study period. However, the year following the 2015 drought had the lowest trout abundance, suggesting a delayed response. This could be affected by potential poor recruitment (Age 0) in 2015 that resulted in lower densities of adult (Age 1+) trout in 2016. At the same time, 2016 also had the fastest annual growth rate and highest condition score, suggesting a compensatory response of growth (Elliott 2015). The drought of 2018 seemed to have different influences on abundance, growth rates, and conditions than the drought of 2015. In 2018, there were no apparent effects on trout abundance the following year. Also, growth and condition of trout in 2018 were among the highest in our study, but they were reduced the following year. The drought of 2019 was the second consecutive drought in our study period, supporting one of the lowest growth rates and condition scores. Collectively, differential legacy effects of drought can influence population trajectories over time as is shown here and in other nearby streams (Kaylor et al. 2019). Many questions remain about the role of extensive and consecutive droughts versus single extreme droughts in population dynamics (Bell et al. 2000). Long-term ecological research is critical to answering these questions (Lobón-Cerviá 2009; Elliott 2015), as it has demonstrated in documenting rare events, legacy effects from previous events, and the resulting biotic responses (e.g., Dodds et al. 2012).

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