

Do precipitation extremes drive growth and migration timing of a Pacific salmonid fish in Mediterranean-climate streams?

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Abstract. Climate change is expected to increase weather extremes and variability, including more frequent weather whiplashes or extreme swings between severe drought and extraordinarily wet years. Shifts in precipitation patterns will alter stream flow regimes, affecting critical life history stages of sensitive aquatic organisms. Understanding how threatened fish species, such as steelhead/rainbow trout (*Oncorhynchus mykiss*), are affected by stream flows in years with contrasting environmental conditions is important for their conservation. Here, we report how extreme wet and dry years, from 2015 to 2018, affected stream flow patterns in two tributaries to the South Fork Eel River, California, USA, and aspects of *O. mykiss* ecology, including over-summer fish growth and body condition as well as spring out-migration timing. We found that stream flow patterns differed across years in the timing and magnitude of large winter–spring flow events and in summer low-flow levels. We were surprised to find that differences in stream flows did not impact growth, body condition, or timing of out-migration of *O. mykiss*. Fish growth was limited in the late summer in these streams (average of 0.02 ± 0.05 mm/d), but was similar across dry and wet years, and so was end-of-summer body condition and pool-specific biomass loss from the beginning to the end of the summer. Similarly, *O. mykiss* migrated out of tributaries during the last week of March/first week of April regardless of the timing of spring flow events. We suggest that the muted response to inter-annual hydrologic variability is due to the high quality of habitat provided by these unimpaired, groundwater-fed tributaries. Similar streams that are likely to maintain cool temperatures and sufficient base flows, even in the driest years, should be a high priority for conservation and restoration efforts.

Key words: drought; growth; headwaters; migration; *Oncorhynchus mykiss*; salmonids; stream flows.

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INTRODUCTION

Drought can have complex effects on stream ecosystems and the ecology of the aquatic species who depend on them (Matthews and Marsh-Matthews 2003). The recent multi-year drought in California (2012–2016) may be the most severe drought in over 21,000 yr, based on analyses of tree rings (Robeson 2015, Kwon and Lall 2016). It was immediately followed by a series of extremely wet years. Such weather whiplash (sensu

Swain et al. 2018) is expected to become increasingly common in California, including more frequent and severe droughts and floods (Cook et al. 2015, Diffenbaugh et al. 2015). It is unclear how precipitation extremes influence the ecology of aquatic species in this region, particularly sensitive species, but understanding these stream flow–ecology relationships has large conservation implications.

Much of California experiences a Mediterranean climate, with most precipitation occurring

between October and April, followed by warm, dry summers (Gasith and Resh 1999, Bonada and Resh 2013). Beyond pronounced seasonality, another defining characteristic of Mediterranean-climate systems is strong inter-annual variation in precipitation, which alters stream flow patterns in both the wet (winter) and dry (summer) seasons. In winter, stream flow varies considerably both in timing and magnitude of peak flows (Kondolf et al. 2012, Cid et al. 2017). In summer, stream flow varies both in the rate of recession from winter to summer base flows and in the magnitude of base flows (Dralle et al. 2016). Across-season flow variation is thus a hallmark of Mediterranean streams, and this variation in flow was on display when California abruptly shifted between weather extremes from drought conditions in 2012–2015 to extremely wet conditions in 2016–2017.

California represents the southern end of the range for anadromous (ocean-migrating) forms of Pacific salmonids (*Oncorhynchus* spp.). Many population complexes in California are protected under federal and state Endangered Species Acts (Williams et al. 2016), and climate change, including stream flow alterations, threatens their persistence (Wenger et al. 2011, Katz et al. 2013). Life histories of *O. mykiss* are tightly coupled to stream flow patterns across the seasons. Winter stream flows cue the upstream migration and spawning of anadromous adults (Banks 1969, Brown 1990), and spring flow events often cue migration of smolts (ocean-migrating juveniles; McCormick et al. 1998, Achord et al. 2007, Roni et al. 2012, Hall et al. 2016). The low-flow summer season is often limiting for growth and survival of *O. mykiss* in California streams (Hayes et al. 2008, Sogard et al. 2009, Grantham et al. 2012, Hwan et al. 2018) and other arid and semi-arid regions, such as parts of Oregon and Washington (Ebersole et al. 2009). Growth during the dry season can later affect over-winter survival (Ebersole et al. 2006) and life history decisions on the timing of age at out-migration (Satterthwaite et al. 2009, 2012), making summer an important period in the salmonid life history. When stream flow is experimentally reduced during the dry season, growth of *O. mykiss* is also reduced (Harvey et al. 2006). However, how growth varies during the dry season following extreme drought vs. wet winters is unknown.

Here, we explore how precipitation extremes influence the ecology of threatened *Oncorhynchus mykiss* in tributary streams by comparing over-summer growth rates and the timing of spring out-migration among years with different stream flow patterns including extreme drought and wet conditions. First, we use long-term flow records to characterize flow conditions at our study site during the three focal years in the context of the longer-term record. Second, we quantify over-summer growth rates, body condition, and change in pool-specific biomass of *O. mykiss* across three summers including during weather extremes. Finally, we quantify differences in the timing of seasonal movements of *O. mykiss* during years with extreme differences in rainfall magnitudes and, to a lesser degree, timing.

METHODS

Study site

We studied growth and movement of *O. mykiss* in two tributaries to the South Fork Eel River, Elder Creek (16.8 km² in drainage area) and Fox Creek (2.7 km² in drainage area), located within the University of California Angelo Coast Range Reserve in Mendocino County, California, USA (Fig. 1). Both tributaries are well-shaded and groundwater-fed (Dralle et al. 2016), maintaining cool water temperatures throughout the summer months. Both resident and anadromous forms of *O. mykiss* are present in these streams. *O. mykiss* is the dominant fish species, representing >99% of our catches (adult Pacific lamprey, *Entosphenus tridentatus*, were occasionally encountered).

Characterizing flow conditions

Elder Creek is the site of a U.S. Geological Survey (USGS) stream gauge (no. 11475560). We used the USGS mean daily discharge to characterize patterns in stream flow during the 2015–2018 water years (where 1 October 2014–30 September 2015 corresponds to the 2015 water year). Stream flow data have been collected at this station since 1967, providing an opportunity to explore stream flow patterns in relation to the long-term record at this site. Specifically, we calculated the cumulative mean daily discharge for each year on record, and then calculated quantiles for the annual cumulative discharge,

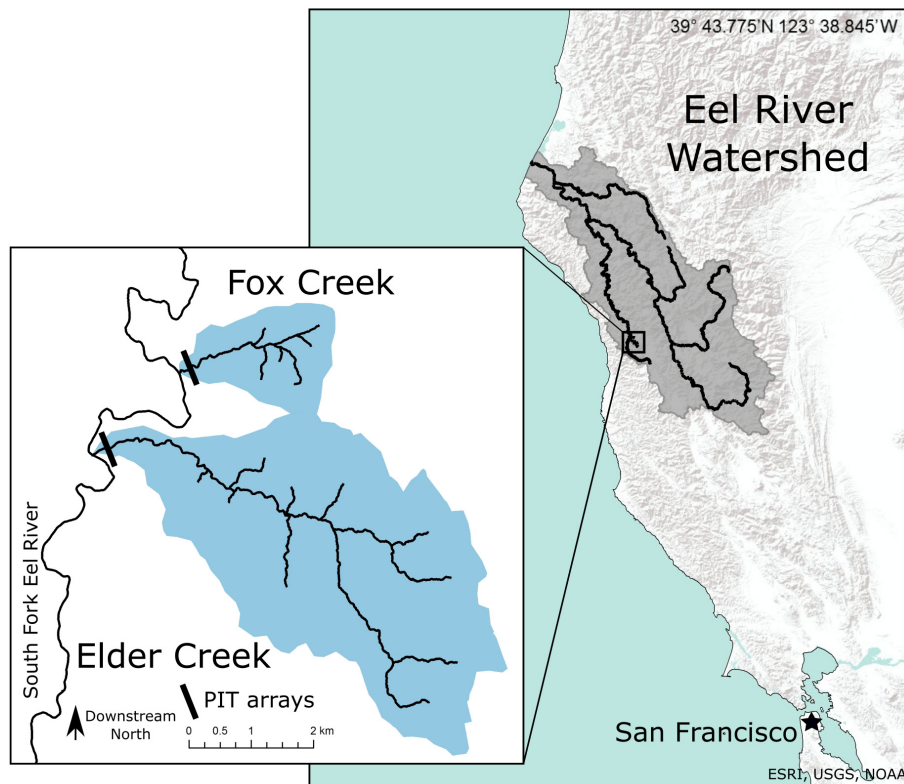


Fig. 1. Fox and Elder Creek are located within the Eel River watershed in northern California, USA.

categorizing years as very dry (1st quintile), dry (2nd quintile), normal (3rd quintile), wet (4th quintile), and very wet (5th quintile; e.g., Kiernan et al. 2012, Hwan and Carlson 2016). Next, we calculated, for each day, the percent difference in discharge from the long-term average for that day, and then calculated the monthly average percent difference in discharge. Fox Creek is ungauged but it is adjacent to Elder Creek (the mouths of the two streams are ~2.5 km apart), and both drain similar geology, so we assumed similar stream flow patterns. To compare summer stream flows in Elder Creek to nearby tributaries in the Eel River watershed, we quantified the summer flows (May–September) as a percent of the winter flows (October–April) for every water year on record. Since there are no nearby, similarly sized, gauged streams, we calculated the same metrics for the South Fork Eel River at Leggett, California, USA (USGS gauge no. 11475800). The mainstem should represent an average of all upstream tributaries (Moore et al. 2015), allowing us to use the mainstem as a

proxy to compare stream flows in Elder to average tributary stream flow patterns.

Fish sampling

We captured *O. mykiss* from ~20% of the pools in both Elder ($n = 140$ –143 total pools surveyed per year) and Fox creeks ($n = 46$ –57 pools per year) from 2015 to 2017. Pools were initially surveyed and mapped onto a 10-m digital elevation map by hand in the field, and then, survey pools were selected using spatially stratified random sampling to encompass all of the habitat occupied by *O. mykiss*. We sampled the same pools every year, with the exception of when winter stream channel dynamics rendered pools inaccessible, in which case we sampled the next upstream pool instead. We blocked the pools with nets at the upstream and downstream ends, and then sampled the fish using three-pass backpack electrofishing, recording effort (number of seconds) for each pass. After fish sampling, the surface area of each pool was estimated by multiplying the maximum length of the unit by the

average wetted width (calculated from five width measurements spaced equally along the length of the pool).

Fish were sampled twice during each summer, once in late-July to early-August (mid-summer sampling, 15 July–5 August 2015; 16 July–5 August 2016; 13 July–3 August 2017), and again in mid-September (late summer sampling, 25–28 September 2015; 9–11 September 2016; 8–10 September 2017), Fig. 2c. Fish were initially captured and marked in the first sampling event when most encountered young of year were large enough to implant with a passive integrated transponder (PIT) tag (over 60 mm in fork length [FL] and 2 g in weight). At capture, fish were measured for FL (mm) and mass (0.01 g), and tagged if large enough. We then returned to a subset of the pools in September to recapture fish, returning to pools where the most fish were PIT-tagged in the July sampling to maximize the possible number of known recaptured fish. We re-sampled 43 pools in 2015, 35 pools in 2016, and 31 pools in 2017. All recaptured fish were re-measured for length and mass, allowing us to estimate end-of-summer growth (hereafter “summer growth”) in each year.

Analyses of fish growth and condition in summer season

We tested for differences in summer growth among years via a series of ANOVAs, with growth rate (mm/d) or mass (g/d) as the response variable and both year and stream (Elder vs. Fox Creek) as predictor variables. All ANOVAs were conducted in R. We explored whether growth was size-dependent using a linear regression with final (late summer) size (FL) as the response variable and initial size as the dependent variable. If the confidence interval for the slope of the regression line included 1, we concluded that there was no size dependence in growth. Additionally, we recaptured a small number of fish during other seasons in sampling for other studies, and we recaptured some individuals across multiple years. For both of these groups of recaptures, we calculated growth rate (mm/d) and qualitatively compared growth rates in other periods with summer growth.

Additionally, we compared fish condition among years for all the fish that were captured during electrofishing surveys in September

($n = 1022$). Specifically, we used ANCOVAs with log mass as the response variable, log length as the covariate, and year as the fixed grouping factor. We first tested for heterogeneity in slopes relating log mass and log length (i.e., the interaction term). If this term was not significant, it was removed and the model was fitted again to explore the influence of the grouping factor (year) and line elevations (i.e., intercepts). When the interaction term was significant, it could not be removed. In these cases, we concluded that condition in one year differed from condition in other years if the log mass was consistently above or below those from the other years. ANCOVA is the preferred method to test for differences in condition factor to appropriately calculate the degrees of freedom and regression coefficients (García-Berthou 2001).

Finally, we compared changes in pool-specific biomass (g/pool) from the beginning to the end of the summer across years. We expected biomass to decline over the summer as this tends to be a period of self-thinning (Dunham and Vinyard 1997), with less biomass per pool in late than early summer, possibly with different rates of declines among years. We used an ANCOVA to test this prediction, with biomass in September as the response variable, biomass in July as a predictor variable, and year as a second predictor variable (fixed effect), and allowed an interaction between year and July biomass.

Additional environmental covariates: temperature and fish density

We explored two environmental correlates of fish growth and condition, water temperature, and fish density. In particular, water temperature can have a strong influence on salmonid growth rates (Myrick and Cech 2005, Boughton et al. 2007). Stream temperatures for Elder Creek (obtained from the USGS gauge and independently measured, S. Kelson, *unpublished data*) followed the same temporal patterns and were similar across all three summers (June–September; Fig. 2d), ranging from a daily mean from 10.6°C to 19.1°C, with an absolute range from 9.7°C to 21.1°C from June to September. The mean water temperatures were slightly higher in 2017, due to a week of warming in September (Table 1, Fig. 2d). Although at times the difference in mean daily temperature was large between years

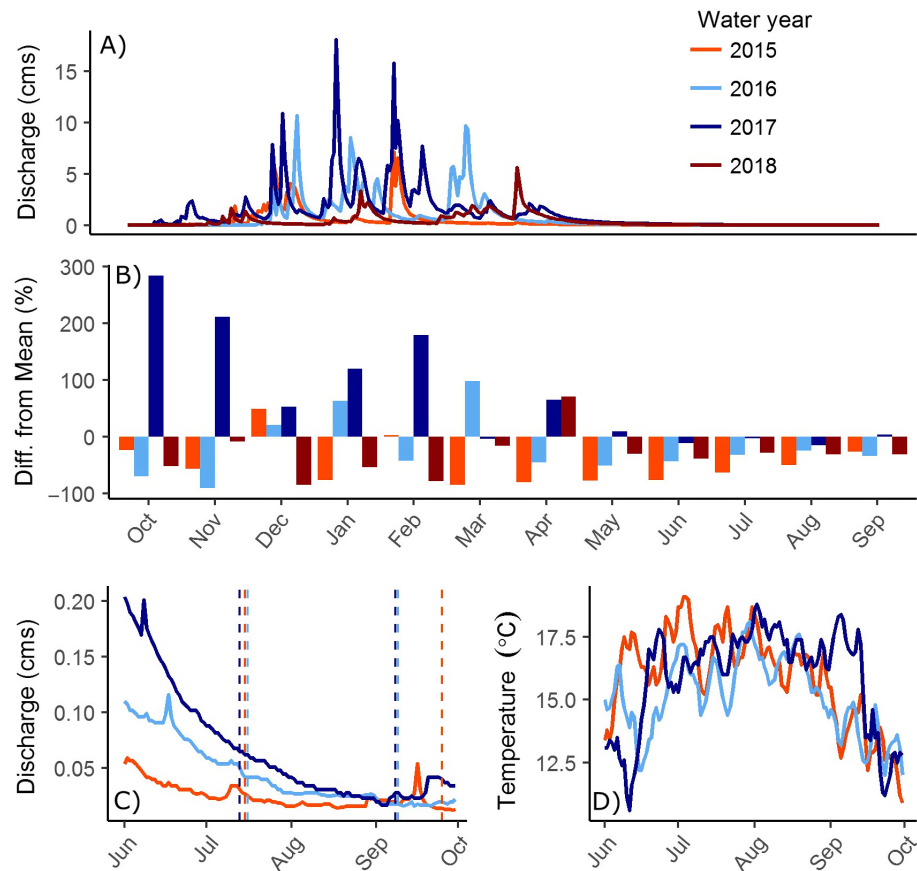


Fig. 2. Differences in winter stream flow for 2015–2018 (when fish migration was monitored) and summer stream flow and temperature for water years 2015–2017 (when fish growth and condition were monitored). (A) Discharge (cms) for the entire year for each year (B) monthly mean percent difference from the long-term (51 yr) daily mean discharge, (C) zoom-in view of discharge in summer months, vertical lines represent start and end of measured growth window for each year and (D) mean daily temperature during the summer months. Data are from USGS Elder Creek Gage (no. 11475560).

Table 1. Mean density of *Oncorhynchus mykiss* in July and stream temperatures during growth measurement window (15 July–30 September).

Year	Density in Elder Creek (fish/m ²)	Density in Fox Creek (fish/m ²)	Stream temperature (°C)
2015	0.36 (0.31–0.41)	0.59 (0.43–0.75)	15.5 (15.1–16.0)
2016	0.31 (0.27–0.35)	0.44 (0.34–0.54)	15.2 (14.8–15.6)
2017	0.28 (0.24–0.32)	0.55 (0.42–0.68)	16.3 (15.8–16.8)

(max. difference of 6°C), the mean difference was low ($2.4^{\circ} \pm 1.3^{\circ}\text{C}$ standard deviation, Fig. 2). Furthermore, the temperatures for all years were well within tolerated thermal ranges

(Wurtsbaugh and Davis 1977, Sloat and Osterback 2013), so we do not analyze temperature as a correlate with fish growth or condition among years.

Density of juvenile salmonids can also have a strong influence on their growth (Grant and Kramer 1990, Jenkins et al. 1999), so we report density estimates from each stream (Fox and Elder Creek) and year (2015–2017) from our July sampling event. We estimated the number of fish per pool using two methods, the total count of fish captured and the Leslie-K method of estimating population size from depletion estimates (Leslie and Davis 1939, Ogle 2016). Differences between these methods were slight (summarized in

Appendix S1), so we present count data. We found that there was no difference in the density of fish captured per pool (fish/m²) among years in Fox or Elder Creek (overlapping 95% confidence intervals, Table 1), and this pattern was the same with density reported as fish/m (Appendix S2: Table S1). Because we did not find inter-annual variation in densities in our sampling reaches, we do not further explore the influence of density on fish growth and condition.

Fish movements during Spring months

To characterize the downstream movements of PIT-tagged fish, we installed stationary antennas that spanned the wetted channel near the mouth of Elder Creek in November 2014 and at the mouth of Fox Creek in May 2015. At Elder Creek, we installed antennas 200 and 350 m upstream of the mouth. At Fox Creek, we installed antennas 175 and 195 m upstream of the mouth. Test tags, which exposed a PIT-tag to the antenna every 30 min, were installed at each antenna to monitor efficiency. For every fish that was detected at the antenna, we received data on the date and time of detection, allowing us to quantify differences in movement patterns across years with different flow conditions. While some movement was detected in most months of the year, we focus here on the spring movements (01 February–31 May), which coincide with the typical out-migration season for anadromous *O. mykiss* in this region (Brown 1990) and when smolt traps are operated in nearby watersheds (Gallagher et al. 2014, Obedzinski et al. 2017).

We grouped detection records from each antenna array into three categories. The first category is perfect detections, or fish that were detected at both upstream and downstream antennas within a 36-h window, signaling directional downstream movement ($n = 98$ fish in the spring at Elder, and $n = 29$ in other months, and $n = 0$ at Fox). The second category represents fish that were detected multiple times at one or both antennas, but with a long (>36-h) gap between detections, suggesting local movement in the vicinity of the antenna array ($n = 16$ at the Elder array, and $n = 8$ fish at the Fox array in spring months, and $n = 15$ and $n = 3$ in other months, respectively). To be conservative, these individuals were removed from our analyses.

The third category represents fish that were only detected at one antenna, or single detections. Due to technical difficulties with antenna operation (e.g., elevated stream flows, debris, shed tags masking the ability of other tags), many of our data points are single detections ($n = 142$ at Elder and $n = 33$ at Fox in the spring, and $n = 55$ and $n = 13$ in other months). We assumed that these spring-season single detections were associated with downstream movement for several reasons. First, all perfect detections during the migration time period were documented swimming in a downstream direction through the array. Second, all of the single detections occurred when only one antenna was functioning. Third, there was no difference in the body length or initial capture location for single detections and perfect detections.

To test for differences in timing of spring fish movement among years, we conducted an ANOVA with Julian date of detection at the antenna array as the response variable and year as the dependent variable. Additionally, we tested whether fish moved during only a subset of the flows, for example, during high flows (Raymond 1988, Jager and Rose 2003). We found that fish moved during both spring and fall (see *Results*), so we tested for movement-flow preferences separately in each season. To test for flow preferences, we compared the flows when fish were moving to all flows available to the fish during the out-migration season, excluding days when the antenna was not operating (at least 50% detection efficiency of the marker tag in order to be designated an operating day). Specifically, we conducted an ANOVA between movement flows and all flows, nested within each year (i.e., year is included as a random effect), separately for both the spring and the fall.

RESULTS

Weather extremes and inter-annual variation in stream flow

This study spanned years with substantial variation in annual precipitation in California, with conditions in the South Fork Eel River watershed ranging from extreme drought conditions (2015 summer, in exceptional drought) and extreme wet conditions (2017 summer, with no drought conditions) according to the U.S.

Drought monitor (<http://droughtmonitor.unl.edu/>). Stream flow in Elder Creek reflected these weather extremes. The 2015 water year was classified as dry (0.22 percentile, compared to long-term record for this gauge), the 2016 water year as wet (0.68 percentile), the 2017 water year as very wet (0.94 percentile), and the 2018 water year as dry (0.24 percentile). Flow differences among these years were greatest in the winter season, from October to April. During the dry 2015 water year, for example, the only month that experienced above-average flows was December, meaning that flows were below-average for the entire out-migration season (February–May, Fig. 2a, b). In the second dry year, 2018, the only month that experienced above-average flows was April, which coincided with the out-migration season (Fig. 2a, b). In the wet year, 2016, only three months experienced above-average flows, December, January, and March, meaning flows were below-average for most of the migration season (Fig. 2a, b). In the very wet year, 2017, flows were above-average for almost the entire wet season, and exceeded the long-term average in February by nearly 200%, then dropped to just below-average (−4%) only in March (Fig. 2b).

There were also differences in summer flows among years, though the differences were muted compared to wet season differences. For the three years that we monitored summer growth rates (2015–2017), the summer flows (June–September) were lower than the monthly long-term average (Fig. 2b), except for September 2017, when flows were slightly higher than the long-term average (+3% difference). Stream flows at the start of summer (on 1 June) differed among years, ranging from 0.05 cubic meters per second (cms) in 2015 to 0.20 cms in 2017, with 2016 intermediate at 0.11 cms (Fig. 2c). In 2017, discharge did not decrease to 0.05 cms until 23 July. Early season differences persisted through mid-summer: On 1 August, discharge was 0.02, 0.03, and 0.04 cms, in 2015, 2016, and 2017, respectively. However, by the end of summer, on 1 September, discharge had converged to 0.02 cms in all years (Fig. 2c).

Summer stream flows in Elder did not decline from winter flows as much as stream flows in the mainstem South Fork Eel River (a proxy for average tributary conditions in the watershed).

Summer stream flows were on average 14.3% \pm standard deviation (SD) 13.5% of winter flows in Elder Creek, while in the South Fork summer stream flows were on average 10.9% \pm SD. 10.6% of winter flows. The average difference of summer flows as a percent of winter flows between Elder Creek and the South Fork was 3.0% \pm SD 4.0%.

O. mykiss growth rates

We recaptured a total of 217 individuals ($n = 63, 85,$ and 69 in 2015, 2016, and 2017, respectively; length and weight histograms in Appendix S2: Figs. S4, S5) from which we calculated summer growth. Overall, *O. mykiss* grew little, and some even lost weight, during late summer regardless of differences among years in stream flow conditions (Figs. 3, 4; Appendix S2: Fig S1). Mean growth rate across all years during this time period was 0.02 ± 0.05 mm/d. Growth rates did not differ between Fox and Elder creeks (site was not a significant effect in a two-way ANOVA within a given year, $P > 0.10$), so growth data from both streams were combined for analyses. Despite differences in initial summer flows across years (Fig. 2c), there were no differences in growth rates among years (i.e., year was not statistically significant in an ANOVA). This finding was consistent regardless of whether growth was measured as length change ($F_{2, 214} = 1.81, P > 0.17$, Fig. 3) or mass change ($F_{2, 211} = 2.70, P = 0.07$; Appendix S2: Fig S1). While growth was negligible overall, small fish were more likely to experience positive growth compared to large fish (slope of regression of late summer length vs. early summer length was <1 ; 95% Confidence Interval of the slope = $0.96\text{--}0.98$), and the regression line intercepted the 1:1 line at 120 mm; Appendix S2: Fig. S2.

Based on a small sample of recaptures at other times of the year ($n = 119$), we found that positive growth occurred outside of the summer season, with the mean growth rate for the entire year of 0.09 ± 0.04 mm/d. Data from 3 fish captured in Fox Creek indicated that growth was very high in the spring and early summer (0.24 ± 0.02 mm/d, from 29 April 2017 to 14 July 2017). We also found that growth rates were high in the early summer (June–July: average of 0.08 ± 0.07 mm/d based on 20 fish from Elder

Creek) and high in the winter (0.12 ± 0.10 mm/d, based on 4 fish captured 24 January 2015, 3 of which were recaptured on 16 July 2015, 1 of which was recaptured on 17 June 2015). A spaghetti plot showing growth histories for all recaptured individuals further highlights that

later summer is generally a period of slow growth compared to other seasons (Fig. 4).

O. mykiss condition factor and declines in pool-specific biomass

We found that fish condition in September differed among years (year was significant in an ANCOVA as well as FL-year interaction; main effect: $F_{2, 1004} = 8.2$, $P < 0.001$, interaction: $F_{2, 1004} = 7.9$, $P < 0.001$). We found that the fish sampled in 2016 were lighter for their length (in worse condition) than the fish sampled in 2015 within the entire size range of fish that we observed (Fig. 5), and they were lighter than the fish sampled in 2017 for most of our observed size range (up to 142 mm, which includes 96.1% of the sampled fish). Fish sampled in 2015 were always heavier than the fish sampled in 2017 within the size range that we observed, but the predicted estimates for weights were very similar between these two years (e.g., overlapping lines in the ANCOVA, Fig. 5), indicating that condition was similar for fish between these two years.

Study pools at the end of the summer had less fish biomass than at the beginning of the summer (July biomass was a significant predictor of September biomass in an ANCOVA, $F_{1, 104} =$

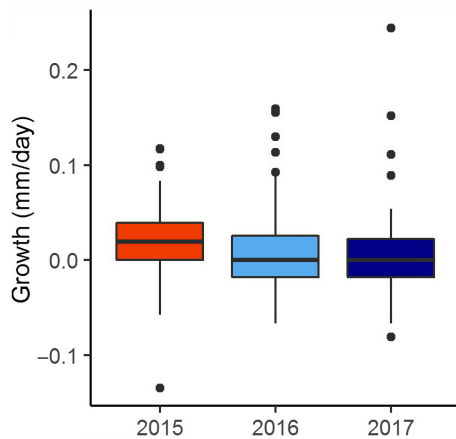


Fig. 3. Individual growth rates (change in length per day) from mid-summer (July) to late summer (September) are close to zero and do not differ between dry (2015, orange), intermediate (2016, light blue), and wet years (2017, dark blue).

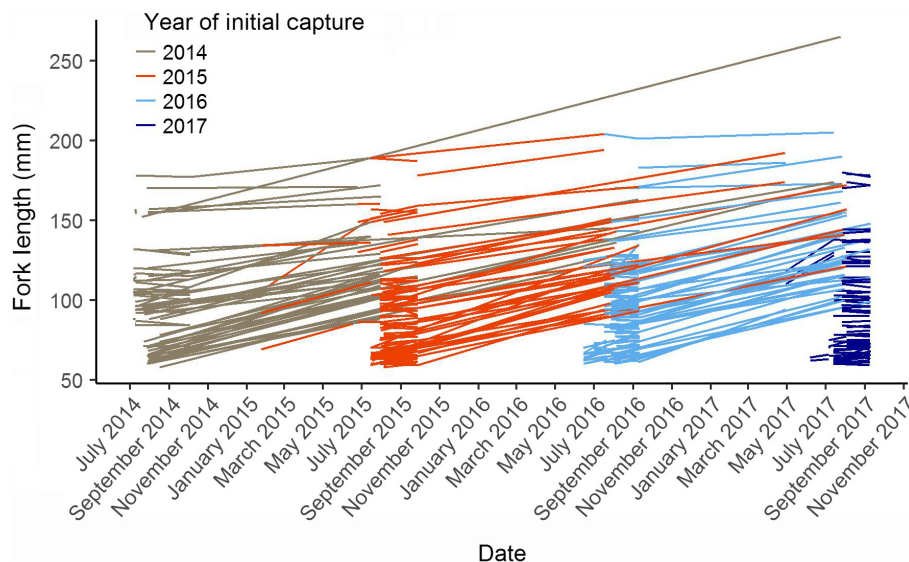


Fig. 4. In Fox and Elder Creek, *Oncorhynchus mykiss* grew over the year between captures over the summer, but did not grow between mid-summer (July–August) and late summer (September). Each line is an individual fish. A positive slope indicates growth, and a flat or negative slope indicates no growth. Tan lines are fish that were initially captured in 2014, orange in 2015, light blue in 2016, and dark blue in 2017.

126.7, $P < 0.01$, and the slope was less than 1, slope estimate \pm standard error = 0.42 ± 0.12), suggesting mortality occurred over the summer. However, the rate of biomass loss from the beginning to end of the summer did not differ among years (i.e., interaction term between year and July biomass was not significant, $F_{2, 104} = 2.4$, $P = 0.09$).

Spring movements and selecting flows for movement

The mean date of all spring movements (defined here as antenna detections between 01 February and 31 May) did not differ among years ($F_{3, 270} = 0.67$, $P > 0.1$ in an ANOVA, mean date 1 April 2015, 28 March 2016, 25 March 2017, and 27 March 2018, Fig. 6) despite extreme differences in flow conditions during this window (Figs. 2, 6). In general, movements were detected from February through May, with most movement concentrated in March and April (Fig. 6, 73.8%, 63.2%, 76.5%, and 84.6% of movements in 2015, 2016, 2017, and 2018, respectively).

Stream flow on the days in which fish were detected moving was significantly higher than the flows available to the fish across the entire spring out-migration season (ANOVA, nested within water year, $F_{1, 713} = 28.1$, $P < 0.01$, Fig. 7). However, this difference in flow was small, and the mean flow when fish were moving was only slightly higher than the mean available flow in any given year (Table 2).

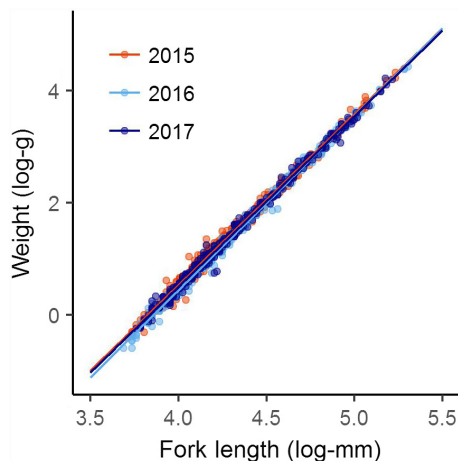


Fig. 5. Length-by-weight relationship (condition factor) for fish caught September does not differ substantially between years (2015, orange; 2016, light blue; 2017, dark blue).

Movements outside the Spring Window

Detections at the stationary antenna revealed an additional pulse of downstream movement outside the spring out-migration season. Most detections at the stationary antenna occurred in the spring months. However, during fall 2016, there was an additional pulse of movement, with 41 fish being detected at the antenna between September and November. These fish were smaller than fish that moved out in the spring ($t_{86} = -4.06$, $P < 0.01$ in a Welch's two-sample t -test), and 93% of these fish were originally captured low in the system (within 0.5 km from the mouth), which differed from the spring detections, 50% of which were originally captured in the lower watershed. Additionally, fall movements were strongly related to stream flow; the stream flow on days when fish were detected moving was significantly higher than the stream flows available to the fish during the fall season (ANOVA, nested within water year, $F_{1, 215} = 10.0$, $P < 0.01$; Appendix S2: Fig S3).

DISCUSSION

California experienced a weather whiplash in 2015–2018 with extreme swings in annual precipitation over a short time span, a phenomenon that is expected to become more common in the future (Swain et al. 2018). In the wettest year (2017), stream flow in Elder Creek in the mid-summer was nearly three times higher than during the driest year (2015). Given the differences in total rainfall among years, we expected that fish growth would differ as well, especially considering that the period of summer that we monitored can be an especially harsh period for salmonids rearing in streams (Hwan et al. 2018). Regardless, we found little difference in growth rates among dry and very wet years. Additionally, spring migration timing differed little between drought and wet years, despite large differences in stream flow during these months. We suggest that groundwater-fed tributary streams with lithology that tends to store water in the critical zone, such as Elder Creek (Rempe and Dietrich 2014, 2018), and provide relatively consistent stream flows, are likely to have muted biological responses to extreme droughts. As follows, these groundwater-fed streams with water-storing lithology may be important sites for

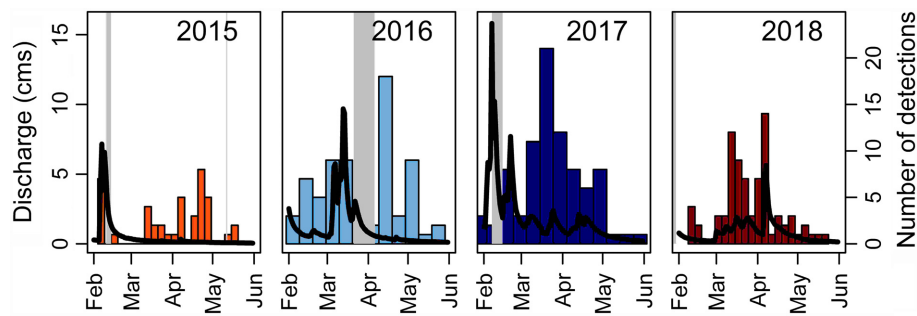


Fig. 6. Peak spring out-migration of juvenile *Oncorhynchus mykiss* occurs at the same date in dry and wet years, from February to May for each water year, 2015–2017. Gray bars indicate when antenna was not operating. Colored bars are the number of detected fish (2015, orange; 2016, light blue; 2017, dark blue; 2018, dark red), and black lines are stream flows.

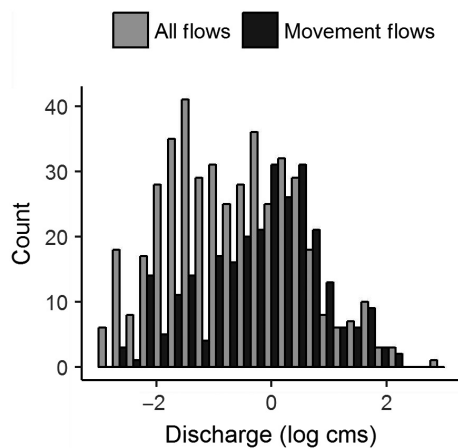


Fig. 7. *Oncorhynchus mykiss* were detected moving at flows that were slightly higher than all the stream flows for the spring seasons. Flows that fish are detected moving at are in black, and all flows for the season are in gray.

conservation of salmonids, especially near the southern end of their range.

Shaded, groundwater-fed tributary streams as high-quality habitat across years

Our result that *O. mykiss* summer growth differed little following wet vs. dry winters is surprising given that previous studies have documented that drought and reduced stream flow can be limiting for salmonids (Elliot et al. 1997, Deegan et al. 1999, Nislow et al. 2004, Harvey et al. 2006), including during the same drought period of 2015 in a snow-melt-dominated stream in Oregon State (VerWey et al. 2018). Similarly,

Table 2. Mean flows (\pm standard deviation [SD]) when fish were detected moving past stationary antenna vs. mean of all flows (\pm SD) when antennas were operating in spring months (February–May).

Year	Movement flows (cms)	All flows (cms)
2015	1.00 (1.94)	0.41 (1.05)
2016	1.15 (1.65)	1.10 (1.75)
2017	1.74 (1.39)	1.61 (1.92)
2018	1.38 (0.96)	0.81 (0.80)

we found minimal differences in trout condition and pool-specific loss of biomass among years. Harvey et al. (2006) experimentally reduced stream flow by 75–80% during summer months and found a concomitant decrease in the growth of juvenile *O. mykiss*. One possible explanation for our results showing little difference among years is that stream flow at the end of the time period (September) was very similar for all three years, despite extreme differences in antecedent rainfall and early summer flow conditions (Fig. 2). These conditions contrast with the experimental manipulation in Harvey et al. (2006), where flows were reduced for an entire 6-week period in the summer when growth was measured, not just the beginning of the sampling period. Moreover, stream temperatures were similar and remained largely within a suitable range for *O. mykiss* across all years in our streams (e.g., 17–19°C, Wurtsbaugh and Davis 1977, Myrick and Cech 2005), which is not true of all rearing streams in California (Boughton et al. 2007, Brewitt et al. 2017).

The convergence of stream conditions at the end of the summer following both dry and wet winters suggests that in some geologic settings, groundwater-fed, shaded tributary habitats can produce sufficient stream flow and cool temperatures to support rearing salmonids during the summer drought season, regardless of the previous winters' precipitation patterns (Rempe and Dietrich 2018). We emphasize that this relative consistency in stream conditions is not the case for all tributaries within a watershed. For example, nearby streams in the Eel River watershed that differ in their underlying lithology become more disconnected (intermittent, with reaches of dry stream bed) over the summer months compared to Elder Creek (Lovill et al. 2018), in addition to having less subsurface water storage and summer base flows (Dralle et al. 2018). Furthermore, Elder Creek has very coarse substrate, consisting of boulders and cobbles, which provides suitable over-summer habitat for salmonids (Suttle et al. 2004, Teichert et al. 2010). Future research that investigates over-summer growth of salmonids in relation to summer base flows across many streams, including streams with lower base flows and smaller substrate, could be important for predicting the effects of drought across broader spatial scales and in different geologic contexts. Here, we highlight the importance of groundwater storing tributaries with suitable substrate as the envelope of suitable conditions for salmonids in California shrinks with climate change (Wenger et al. 2011). Many upper headwater tributary sites are disconnected from each other and mainstem habitats, and restoring access to these sites, by barrier removal or redesign (Kemp and O'Hanley 2010, Martens and Connolly 2010), could facilitate access by salmonids to high-quality habitat (Fausch et al. 2002b, 2009, Sheer and Steel 2006).

Summer growth is minimal in Mediterranean-climate California streams

Our finding that growth is minimal during the summer season in Mediterranean-climate California streams is in agreement with other studies that have measured growth rates of *O. mykiss* in coastal California streams (Harvey et al. 2005, Sogard et al. 2009). Our study is also consistent with the results of Hayes et al. (2008), who also

found little to no growth of *O. mykiss* between August and September in Scott Creek, California (Santa Cruz County), and that growth rates did not increase until November in. Similarly, Harvey et al. (2005) found low specific growth rates of *O. mykiss*, between -0.2% and 0.6% , in the summer in Jacoby Creek, Humboldt County, California. In another stream in Santa Cruz County, California, Soquel Creek, the fastest growth rates for *O. mykiss*, were observed in winter (Sogard et al. 2009). There, summer growth rates were much higher than our estimates (0.11 vs. 0.02 mm/d), but they measured growth during summer over a longer period, including June–October, and it is possible that fast growth in early summer or the fall wet-up contributed to the observed summer growth. These studies, together with the data we present on a few individuals who were recaptured during the early summer period, suggest that the early summer (June–July) may be a time of elevated growth and productivity, but that growth slows as the summer progresses.

Reduced growth at the end of the summer for salmonids rearing in Mediterranean-climate streams may be linked to food web phenology during this season. In the Eel River, food web productivity, including invertebrate biomass, peaks early in the summer, often from June to July (S. Kelson, *unpublished data*, McNeely and Power 2007, Power et al. 2008), a pattern that is common among semi-arid streams that experience reliably dry summers (Rundio and Lindley 2008). The reduction in invertebrate biomass, in addition to the reliable reduction in stream flows (even in summers following extreme wet years, such as 2017), may result in limited opportunities for drift feeding during this period, which is one of the primary feeding behaviors exhibited by juveniles salmonids rearing in streams (Fausch 1984, Nielsen 1992, Nakano and Kaeiryama 1995). Experimental manipulations of food availability in other systems have greatly increased growth rates, by up to $0.9\%/d$ in *O. kisutch* (Rosenfeld et al. 2005) and up to $2.3\%/d$ in *O. mykiss* (Boughton et al. 2007), suggesting that food availability is limiting in natural streams, and may be a cause of reduced growth. However, pulsed subsidies from the mainstem (Uno and Power 2015) or the terrestrial environment (Nakano and Murakami 2001, Fausch et al.

2002a) may compensate for reduced instream production.

While growth was negligible overall, there was a slight tendency for the smallest fish to show positive growth, suggesting that smaller individuals may be better able to withstand the harsh late summer conditions. For young fish, summer growth and body condition are linked to overwinter survival (Ebersole et al. 2006, Evans et al. 2014) and downstream life history decisions (Satterthwaite et al. 2012), which may influence their motivation to feed during late summer despite the increased effort required to acquire food in low-drift and low-flow conditions (Caldwell et al. 2018).

*Stream flow and timing of *O. mykiss* movements*

Beyond limited differences in growth, we found that the timing of when juvenile *O. mykiss* moved downstream in spring was similar among years. Fish moved during all flow conditions available during the spring, showing only slight (but significant) preference for higher flows. These results suggest that juvenile trout migrating from Elder and Fox creeks are not limited by flow during the spring migration window, even during the recent drought years. In other California streams, especially streams with low gradient riffles, emigration of smolts can be limited by the riffle crest depth (Holmes et al. 2016). Future research could leverage smolt trap data from life cycle monitoring efforts to explore how the timing of migration differs across many streams in California between drought and flood years, including in streams that tend to be limited at the riffle crest vs. those characterized by high spring base flows and water depths. Furthermore, our results contrast with other research indicating that high flow events can cue fish migrations (Jonsson 1991). We should note that the antennas were often not functional during the highest flows, and we could have missed movement pulses during those periods. Previous studies have found that juvenile salmonids likely initiate migrations in response to various cues, including photoperiod and stream temperature (Bjornn 1971, Achord et al. 2007, Spence et al. 2014) and lunar cycles (Grau et al. 1981, DeVries et al. 2004). Understanding the conditions under which stream flow does and does not cue smolt migration or limits the movement of

out-migrating smolts is a rich topic for future research, particularly given the uncertainty in the timing of winter storms under climate change (Dettinger 2011).

While we did not find flow-initiated migrations in the spring season, we did find a pulse of downstream movement during elevated flows in the fall. Across our three years of study, there were several early season storms in only one year (fall 2016), and in this year, we also detected individuals moving past stationary antenna. Fall movements have been previously documented for juvenile *O. mykiss* (Brown 1990, Tattam et al. 2013) and other anadromous salmonids (Riddell and Leggett 1981, Roni et al. 2012). In Washington State, these fall movements were associated with the larger, faster growing individuals who were moving into higher-order streams (Tattam et al. 2013), likely because these individuals did not have the lipid stores to survive in cold tributaries over the winter. Here, we found that the individuals who moved in fall were smaller on average than those moving in the spring, and they originated from the lower watershed in Elder. These patterns suggest that the fall movers may be subdominant compared to those who are moving in the spring (Sloat and Reeves 2014), and either shuffling habitat units within the creek, volitionally moving downstream to rear in the mainstem, or being displaced with the high flow pulses (Young et al. 2011).

*Drought, weather whiplashes, and *O. mykiss* ecology*

Although we did not find a large effect of drought flow conditions on *O. mykiss* summer growth or spring out-migration timing, there may have been changes to steelhead juvenile ecology and performance that we did not measure. For example, we did not quantify survival in this study. While we found little difference in late summer fish density among years, it is possible that this reflects earlier self-thinning or significant mortality differences among years, and thus improved growth opportunities for survivors (Dunham and Vinyard 1997, Keeley 2003). Additionally, nearby habitats that are also used by juvenile *O. mykiss*, such as the mainstem South Fork of the Eel River, can be quite warm during the summer (up to 28°C), and those warmer conditions are associated with higher

incidence of black spot disease (Schaaf et al. 2017). Moreover, drought years without a scouring flood event produce a food web that is less favorable for salmonids feeding in the mainstem South Fork Eel River (Power et al. 2008, 2013). In other streams, and especially further south in the range of anadromous *O. mykiss*, reduced flows are often correlated with increased stream temperatures that create physiologically stressful conditions for cold-water salmonids (Mantua et al. 2010, Wenger et al. 2011, Boughton et al. 2015).

CONCLUSIONS

Overall, we report that *O. mykiss* growth and movement did not differ across years, despite an abrupt transition from extreme drought to wet years. These results highlight the importance of upper headwater streams with water-storing lithology that leads to maintained summer base flows (Rempe and Dietrich 2014, Dralle et al. 2018) and stream connectivity (Lovill et al. 2018) for buffering biological responses to extreme drought. These habitats may be especially important for conserving salmonids in semi-arid environments, making them a high priority for conservation and restoration efforts (Wenger et al. 2011, Katz et al. 2013).

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5p464rm>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2618/full>