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Source: Northwestern Naturalist, 99(3):209-221.

Published By: Society for Northwestern Vertebrate Biology

<https://doi.org/10.1898/NWN17-27.1>

URL: <http://www.bioone.org/doi/full/10.1898/NWN17-27.1>

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EFFECTS OF A SEVERE DROUGHT ON SUMMER ABUNDANCE, GROWTH, AND MOVEMENT OF CUTTHROAT TROUT IN A WESTERN OREGON HEADWATER STREAM

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ABSTRACT—Winter snowpack depth, snowmelt timing, and snowmelt duration are projected to change in the future, leading to increased frequency and severity of drought in the Pacific Northwest. In summer 2015, stream flows throughout the Pacific Northwest were at record low levels because of low winter snowpack conditions consistent with these climate projections. We explored effects of the 2015 low-snowpack-associated drought on Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) abundance, growth, and movement patterns in two 100m reaches (<60 y and >350 y old forests) of an unnamed perennial western Oregon headwater stream before (2 y) and during a severe drought. We found that the abundance of Cutthroat Trout declined substantially during the drought year, regardless of habitat availability, riparian forest age, or stream wood structure. Fish growth during summer was consistently negative during all 3 y of the study in both reaches. During the drought year, estimated abundance and total biomass of Cutthroat Trout declined in both reaches compared to the 2y prior. In all 3 y, the majority (76%) of fish in the reach with a young riparian forest stand moved >2 m from their release point. In contrast, across the 3 study years, only 26% of fish on average moved >2 m from their release point in the old-growth reach, which had more large wood and pool area. Across both reaches, in the non-drought years, most fish moved into pools (32.4%), but some moved to riffles (23.3%). During the drought year, of the fish that were recaptured, only upstream movement to pools were observed. There were no observed movements of recaptured fish to riffles. Overall, study results suggest that increasing severity of summer drought in the Pacific Northwest is likely to reduce the abundance of fish in small headwater streams, and the remaining fish preferentially use pool habitats such as those found in structurally complex streams.

Key words: Cutthroat Trout, drought, fish movement, growth, headwater stream, *Oncorhynchus clarkii clarkii*, Oregon

Natural disturbances are widely recognized for their importance in structuring stream ecosystems (Resh and others 1988; Lake 2003). In regions with predictable annual hydrologic events, such as seasonal floods and droughts, many biota are resilient to episodic disturbances but remain susceptible to events that exceed normal ranges of variability (Lytle and Poff 2004; Power and others 2013). In the Pacific North-

west, climate change is anticipated to reduce snowpack in mid-elevation drainages, with subsequent increases in the duration and intensity of summer drought conditions (Miles and others 2000; Mote 2003; Mantua and others 2010). As summer discharge declines, decreased flow reduces surface-water habitat and connectivity, which may be particularly important to the biota in small headwater streams (Arismendi

and others 2013). Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) are often the only fish species present in 1st- and 2nd-order headwater streams in the Pacific Northwest, and while trout in these systems are well adapted to a Mediterranean climate with natural low-flow in summer, the frequency and severity of future droughts may create stream conditions that impact the population dynamics and behavior of this species. In this study, we explored how the extreme drought conditions of summer 2015 affected Cutthroat Trout abundance, growth, and movement patterns relative to the previous 2 y in a 2nd-order headwater stream in the western Cascade Range of Oregon.

Studies evaluating the effects of drought in streams have found that these disturbances can reduce the survival, abundance, and growth of resident fish (Berger and Gresswell 2009; Walters 2016). A meta-analysis by Walters (2016) evaluating studies of fish responses to low-flow events found that 74% of studies reported decreased survival-recruitment, 60% reported declines in abundance, and 65% found declines in fish growth and body condition. These responses are often linked to physical habitat changes, including warmer temperatures, lower dissolved oxygen concentrations, and reduced habitat availability (Hakala and Hartman 2004; Walters 2016), as well as increasing inter- and intra-specific competition for limited resources as wetted area shrinks and biota are concentrated into smaller habitats (Powers and others 2013).

Low-flow conditions also influence fish movement in streams (Schmetterling and Adams 2004; Mellina and others 2005). Movement is a fundamental animal behavior that affects ecological processes such as community structure, interspecific interactions, and energy flow through ecosystems (Schmetterling and Adams 2004). Environmental disturbances can alter individual movement, with consequences for an individual's survival, growth, and reproductive success (Hodges and Magoulick 2011; Hilderbrand and Kershner 2004), as well as population persistence and resilience (Pulliam 1988). Therefore, quantifying movement during a disturbance event can improve our understanding of ecological mechanisms that may underlie the maintenance of species populations and the structure of communities in fragmented and increasingly modified landscapes (Mantua and others 2003; Stewart and others 2005).

In small systems such as headwater streams, seasonal changes in water flow shape movement patterns of aquatic vertebrates (Mellina and others 2005). For example, the frequency and magnitude of Cutthroat Trout movement increases in spring in association with spawning, and declines in late summer during periods of low flow (Hilderbrand and Kershner 2000; Mollenhauer and others 2013; Mellina and others 2005). Alternatively, trout movement may increase at the onset of low-flow conditions if individuals attempt to occupy higher quality habitats such as deep pools (Kahler and others 2001), colder water (Dobos and others 2016), or stream reaches less prone to dewatering (Davey and Kelly 2007). Given the results from these studies, in a drought year, one would expect the strongest effects on movement to occur in the smallest headwater streams where connectivity is limited.

In this study, we explored Coastal Cutthroat Trout abundance, growth, and movement responses to an extreme drought event during summer in a headwater ecosystem in the Cascade Range of western Oregon. We sampled an unnamed 2nd-order perennial stream for 3 summers. Summer base flow within the normal range of variability occurred in 2013 and 2014, and extreme low-flow conditions in 2015. Winter precipitation in the Pacific Northwest during 2015 was below average and snowpack was at record low levels through January, February, and March, which in turn led to record low stream discharges in spring, summer, and autumn of that year. Based on studies from Berger and Gresswell (2009) and Walters (2016), we expected reduced trout abundance and growth in 2015 relative to the previous 2 y. Further, we hypothesized downstream bias in trout movement over summer in all 3 y of the study, and that mid-summer movement would be reduced during the drought year.

METHODS

Study Site

We conducted this study in the HJ Andrews Experimental Forest (HJA), located on the west side of the Cascade Range in north-central Oregon (Fig. 1). The HJA was predominantly defined by the drainage basin of Lookout Creek, a 5th order stream. Elevations in the HJA ranged from an elevation of 354 m where Lookout Creek

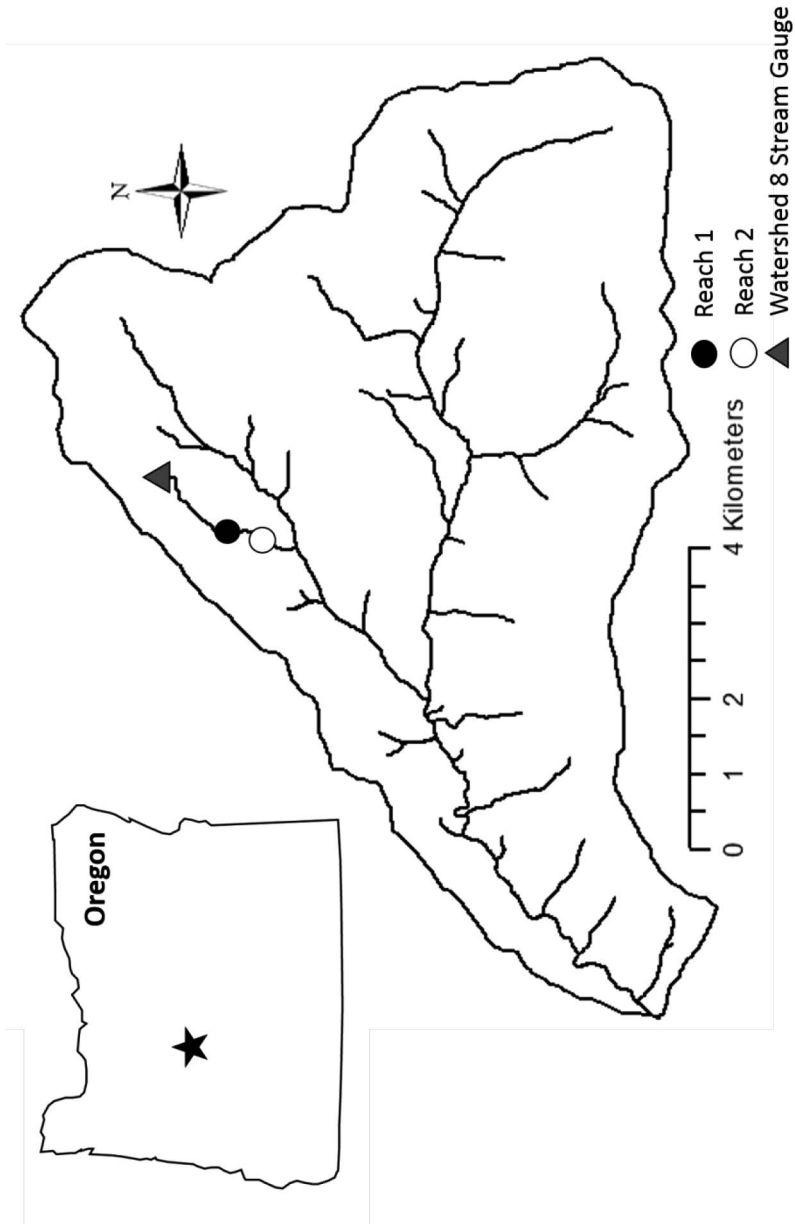


FIGURE 1. A map of the 2 study reaches (black and white circles) and the Watershed 8 stream gauge (gray triangle) in the HJ Andrews Experimental Forest in Oregon.

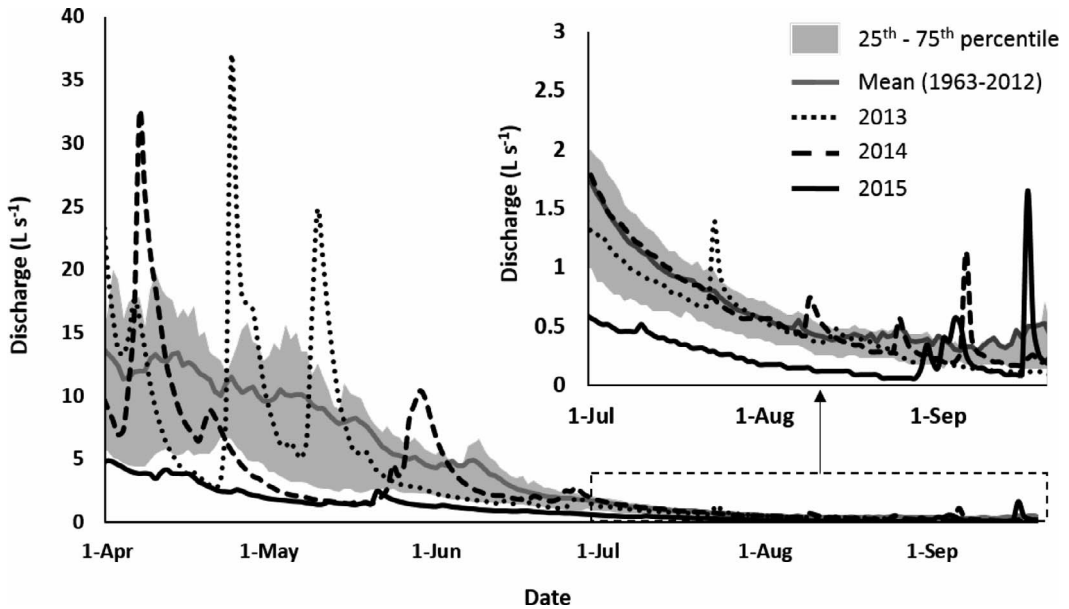


FIGURE 2. Historical discharge at the Watershed 8 headwater gauge at the HJ Andrews Experimental Forest dating from 1963–2012. The shaded grey represents quartiles of the historical data for each day. The dark solid line represents the mean flow for 2015. Dashed lines represent the mean flow during the non-drought years of 2013 and 2014.

entered Blue River Reservoir to 1630 m at the top of Carpenter Mountain. Climate was temperate with a dry summer season and a wet winter season with snow typically accumulating at elevations above 900 m. The HJA forest was dominated by old-growth stands interspersed with areas of 2nd-growth forest regenerating from harvest experiments during the 1950s through 1980s.

The 2 stream reaches we evaluated were on an unnamed 2nd-order perennial tributary draining a western sub-basin of McRae Creek. Reach 1 (100 m in length) was bordered by 2nd-growth stands of Douglas-fir (*Pseudotsuga menziesii*) and Red Alder (*Alnus rubra*) that regenerated naturally following harvest in 1953 (Cut L503-HJA records). Reach 2 (also 100 m in length) was bordered by old-growth riparian forests with dominant Douglas-fir canopy trees >350 y in age. Reach 1 was located approximately 200-m upstream of Reach 2. We selected these 2 reaches because they were both fish bearing, of a similar size, exhibited different degrees of habitat complexity including large wood and pool area, and flowed through 2 distinct forest age classes. Additionally, a monitoring station positioned

1500-m upstream of Reach 1 recorded discharge and temperature data (HJA Watershed 8). Although discharge at this station was lower than in our 2 study reaches, the historical data from this gauge (ranging from 1963 to 2015) allowed us to contextualize in a longer time frame the 3 y over which this study was conducted (Fig. 2).

Habitat Surveys

In 2013, we conducted habitat surveys in each study reach and recorded riparian tree DBH, stream large wood, bank-full and wetted width, gradient, and pool area. Large wood, classified as pieces >10 cm in diameter and 100 cm in length, were counted and the volume was calculated by measuring the length and diameter at both ends. Bank-full and wetted widths were measured every 10 m within each reach and averaged in each year of the study. Gradient was calculated using a Suunto PM-5 clinometer by dividing the change in reach height by the length of the reach. Pools were assessed by measuring maximum depth, outflow depth, length, and width (Table 1). We deployed HOBO® Water Temp Pro v2 temperature loggers (Onset,

TABLE 1. Habitat metrics of Reach 1 and Reach 2 of the study stream (second-order headwater tributary of McRae Creek) in the HJ Andrews Experimental Forest, Oregon, 2013. Reach 1 was located 200 m upstream of Reach 2.

Metric	Reach 1	Reach 2
Reach length (m)	100	100
Riparian forest stand age (y)	60	>350
Reach wetted area (m ²)	153.6	177.5
Large woody volume (m ³)	3.9	44.1
Wetted width (cm)	154	177
Bankfull width (cm)	337	407
Gradient (%)	4.3	5.6
Number of pools	5	11
Pool area (%)	13.1	24.5

Bourne, MA) at the bottom of both reaches and recorded temperature every 15 min for the duration of each study period for each year. We then calculated the average temperature for each day of the study as well as the maximum and minimum average daily temperatures through summer.

We recorded features in the stream that would prohibit fish movement such as dewatered sections, or potential low-flow barriers such as plunge pools >0.75 m in all 3 y of the study. Pools and riffles were the 2 dominant geomorphic habitat types within our study site, and we subsequently defined a habitat unit as a longitudinally distinct pool or riffle sequence.

Fish Collection and Marking Methods

Fish sampling occurred between 6 August and 24 September in 2013, 2014 and 2015. In order to evaluate population metrics such as abundance and growth during summer low-flow periods, we captured fish twice during the summer growing season in each year. Fish were collected with a Smith-Root LR-20b backpack electroshocker (Smith-Root, Inc., Vancouver, WA). For the 1st shocking event, block nets were placed across both the upstream and downstream ends of the reach to close the system between 3 successive, equal-effort passes. All Cutthroat Trout were anesthetized with Aqui-S (Aqui-S New Zealand Ltd., Lower Hutt, NZ), measured to the nearest mm (total length) and weighed to the nearest 0.01 g. For Cutthroat Trout over 60 mm, we injected a Visual Implant Elastomer tag (VIE; Northwest Marine Technology, Inc., Shaw Island, WA) in the subcutaneous tissue under the dorsal fin and behind the left eye. We used

different elastomer tag colors for each reach to determine if fish were moving between stream sections. Cutthroat Trout >70 mm also received a 9-mm HPT9 Passive Integrated Transponder tag (PIT; Biomark, Boise, ID) for individual identification. Tagging fish with both VIE and PIT tags allowed us to measure PIT-tag retention during each year of the study. After being PIT tagged, Cutthroat Trout were released evenly back into the reach, the location of release was recorded, and the block nets were removed. Recapture surveys were conducted using an electroshocker in both reaches 4 to 6 wk after the initial capture. To account for local movement beyond the edges of each reach, we shocked 50 m above Reach 1, 50 m below Reach 2, and the entirety of the 200-m section between the 2 reaches. To enable accurate position measurements of capture and recapture locations of fish, we staked the entire study reach with flags placed every 1 m. Fish were scanned for PIT tags with a hand-held reader when they were caught and the location of capture was noted. All recaptured individuals (any fish with an elastomer tag) were weighed and measured for total length.

Data Analysis

We used the program MicroFish to calculate biomass and abundance of Cutthroat Trout in each reach (Deventer and Platts 1989). Biomass and associated confidence intervals for each reach were calculated by multiplying the maximum likelihood population estimate and abundance confidence intervals by the mean mass of Cutthroat Trout in each respective reach. Juvenile Cutthroat Trout (age-0) and Cutthroat Trout >1 y of age were clearly distinguished based on body length-frequency histograms. These 2 groups were analyzed separately because capture probabilities are often lower for the smaller age-0 fish. Density was calculated using our abundance estimate and associated confidence intervals divided by wetted area. Growth rate was calculated by dividing the change in weight (0.01 g) by the number of days between capture and recapture events. In this study, we defined growth rate as the change in weight during the sampling period. We acknowledge that adult trout in mountain streams may in fact lose weight during summer, and in describing results in the change in mass of recaptured fish, the loss

of weight during the sample period is hereafter characterized as a negative growth rate.

Movement was recorded only for age-1 and older individuals (those large enough to PIT tag). An individual was determined to have "moved" if it was recaptured in a habitat unit (pool or riffle) different than that in which it was released, and it must have been a minimum of 2 m from the original release point. This accounted for the possibility of herding fish with the electroshocker beyond their initial holding location. Upstream movements were given positive values and downstream movements were given negative values. Daily movement was calculated by dividing the absolute value of an individual's movement (to account for "negative" movement downstream) by the number of days between release and recapture. This allowed for standardized movement over time with the slightly different recapture periods. To assess the potential for size to affect movement, focusing on the individuals that moved ≥ 2 m, we regressed the total length of each fish against the absolute value of its movement in summer over all 3 y.

RESULTS

Both riparian and stream habitat varied between Reach 1 and Reach 2 despite their close proximity to each other (approximately 200 m) (Table 1). Reach 1 was bordered by a mixture of 2nd-growth Douglas-fir and Red Alder with a combined average DBH of 22.46 cm, whereas Reach 2 was dominated by old-growth Douglas-fir with an average DBH of 132.75 cm. Large woody debris, % pool area, and gradient were all greater in Reach 2 than in Reach 1 (Table 1).

In 2015, spring and summer stream flows at the HJ Andrews Watershed 8 weir were well below historical levels based on the long-term record dating back to 1964 (Fig. 2). From 1 June until 24 September 2015 (the conclusion of our study), discharge was below the 5th percentile of historical discharge on 62% of days (71 of 116). Discharge was the lowest value on record (over 52 y of record) for 28% of days (46 of 116). The extreme low-flow discharge reduced stream surface water connectivity in 2015. We found a short section of the stream (<2-m longitudinal length) that had no surface water connection in Reach 1. In Reach 2, we found 2 short dewatered sections (4 m total) in 2015. In the 2 previous years, there were no dewatered sections in either

reach. When combining both Reach 1 and Reach 2, average daily stream temperature in August and September was 13.91°C ($SD = 1.42$) in 2013, 13.31°C ($SD = 0.86$) in 2014, and 13.45°C ($SD = 1.64$) in 2015.

Adult Cutthroat Trout abundance was significantly lower in 2015 compared to 2013 and 2014 (significance inferred from lack of overlap between 95% confidence intervals) (Fig. 3a, Fig. 3b). Poor depletion of age 0+ (juvenile) Cutthroat Trout in 2013 resulted in larger confidence intervals around population estimates, which limited our ability to assess significance in the trends in juvenile abundance among the 3 y. Mean total length of adult Cutthroat Trout during the duration of the study was 105 mm, and the maximum total length of any individual was 156 mm.

Overall, most fish lost weight through our summer survey period in all 3 y of this study. Based on an evaluation of overlapping 95% confidence intervals, the mean change in fish weight did not differ significantly among years (Fig. 3c, Fig. 3d). When combining Reach 1 and Reach 2, the percent change in Cutthroat Trout biomass per day was an average of -0.15, -0.13, and -0.08% in 2013, 2014, and 2015, respectively. In 2015, growth in Reach 2 was less negative than in Reach 1, but this difference was not significant ($P = 0.33$).

A total of 50, 60, and 25 individual Cutthroat Trout were PIT-tagged during the summers of 2013, 2014, and 2015, respectively. Of the individuals tagged, 44% ($n = 22$), 63% ($n = 39$), and 76% ($n = 19$) were recaptured each year. In 2013, 50% ($n = 11$) and in 2014, 62% ($n = 24$) of recaptured individuals moved away from the original release point, whereas the remaining individuals ([50%, $n = 11$] and [38%, $n = 15$], respectively) stayed within the habitat unit in which they were released (Fig. 4). During summer 2015, the majority of Cutthroat Trout stayed within the habitat unit in which they were released (68%, $n = 13$), whereas the remaining individuals moved a minimum of 1 habitat unit (32%, $n = 6$).

Cutthroat Trout displayed upstream and downstream movements in both 2013 and 2014, but only upstream movement in 2015 (Fig. 5). In 2013, of the recaptured Cutthroat Trout, 18% ($n = 4$) moved upstream of their release location, and 32% ($n = 7$) moved downstream. In 2014, 44% ($n = 17$) of recap-

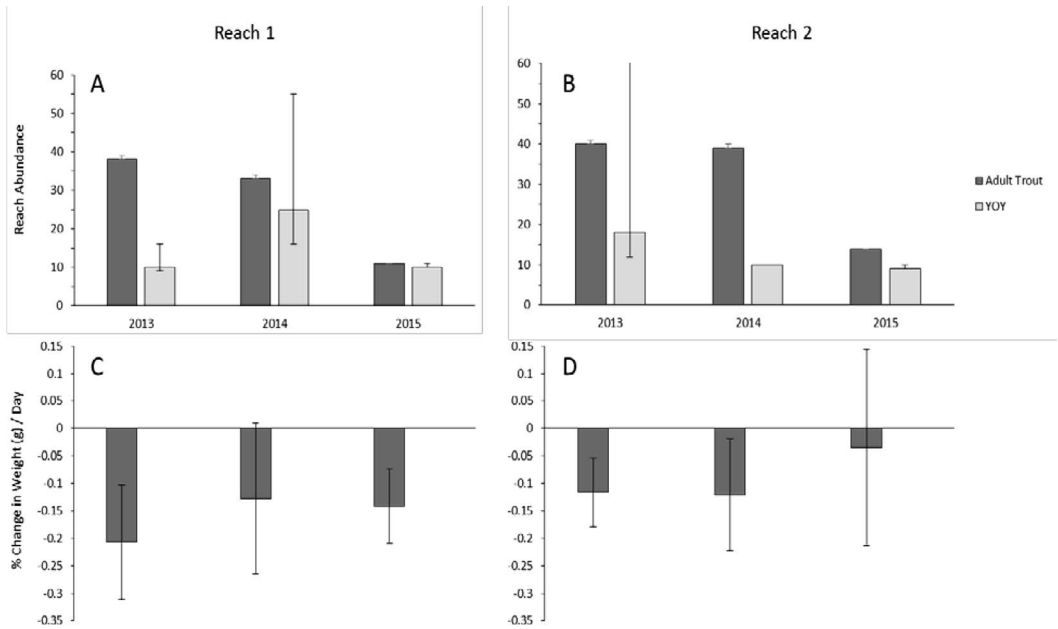


FIGURE 3. Abundance estimates of Cutthroat Trout and Young of Year (YOY) in (A) Reach 1 and (B) Reach 2, and growth rate estimates of Cutthroat Trout in (C) Reach 1 and (D) Reach 2 of a 2nd-order tributary stream in HJ Andrews Experimental Forest. Error bars represent 95% confidence intervals using 1.96 multiplied by the standard error of the sampling mean. Bar colors: light gray = YOY; darker gray = adult trout.

tured individuals moved upstream and 18% ($n = 7$) moved downstream. In 2015, however, 32% ($n = 6$) of recaptured individuals moved upstream, whereas we observed no downstream movement. Comparing differences in movement between the 2 reaches in all 3y, we found that the majority of fish in Reach 1 moved from the habitat unit in which they were released, whereas the majority of fish in Reach 2 did not move from their release point. The maximum distance moved by a recaptured Cutthroat Trout in each year was 44 m, 72 m, and 42 m for 2013, 2014, and 2015, respectively (Table 2). We found no significant relationships between length of tagged fish and the net distance moved (total distance moved including both upstream and downstream movements) during the non-drought years (2013, $P = 0.06$; 2014, $P = 0.47$) or the drought year (2015, $P = 0.63$).

DISCUSSION

Drought conditions were widespread and severe across many regions of the western United States in summer 2015 owing to limited

winter precipitation and extremely low snow-pack (Mote and others 2016). In the 2 reaches of the 2nd-order study stream, we found reduced abundance and a potential shift in summer movement patterns for Cutthroat Trout during the abnormally low discharge year of 2015 compared to the previous 2y in which discharge was notably higher throughout summer. Despite differences in large wood and pool volume between our study reaches, fish abundance in 2015 was consistently lower across both reach types relative to 2013 and 2014. Similarly, fish lost weight on average over all 3 y, although there was a non-significant decline in mean weight loss in the drought year (smaller reductions in weight). Adult Cutthroat Trout movement was also reduced in 2015 with fewer recaptured individuals moving at least 1 habitat unit between summer sampling periods compared to 2013 and 2014. We observed upstream and downstream trout movement in 2013 and 2014, with a similar number of individuals moving upstream and downstream; however, in 2015 all observed trout movement was upstream

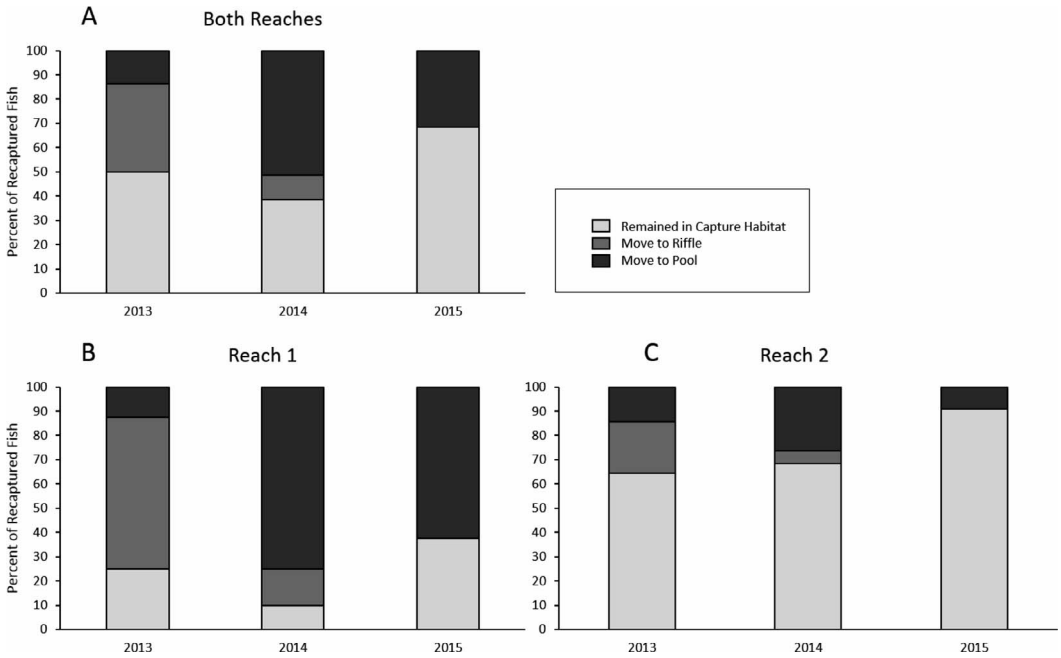


FIGURE 4. Overall proportion of recaptured Cutthroat Trout for all surveys (A), Reach 1 (B), and Reach 2 (C) that stayed at the release point, moved to pools, or moved to riffles in each year of the study. Data represent aggregate results from both reaches on the study stream. Reach 1 flowed through naturally regenerated 2-nd growth (~60y) Douglas- fir forest, whereas Reach 2 flowed through old-growth (>350 y) Douglas-fir forest. Bar colors: light gray = remained in capture habitat; gray = move to riffle; dark gray = move to pool.

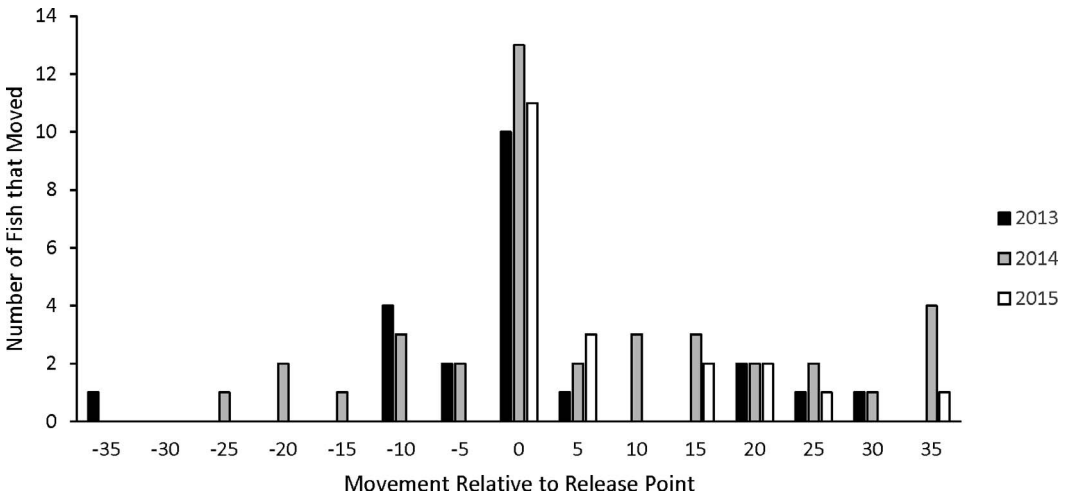


FIGURE 5. Patterns of movement (direction and net distance) of recaptured Cutthroat Trout in 2 non-drought years and 1 drought year. Movement was considered when recaptured individuals were found in a different habitat unit than that in which they were initially released and more than 2 m from the release point. We binned movement in increments of 5 m. Any movement ≥ 30 m was binned as 35 m. Data represent aggregate results from both reaches of the study stream. Positive values denote movement upstream, and negative values denote movement downstream. Bar colors: black = 2013; gray = 2014; white = 2015.

TABLE 2. Movement distances for Cutthroat Trout in Reach 1 and Reach 2 of the study stream (2nd-order headwater tributary of McRae Creek) in the HJ Andrews Experimental Forest. Movement per day was calculated by dividing absolute movement (the absolute value of movement) by the number of days between release and recapture. We did not examine movement of juvenile Cutthroat Trout as we did not PIT tag fish <70 mm.

Age Group	2013		2014		2015	
	Reach 1	Reach 2	Reach 1	Reach 2	Reach 1	Reach 2
Adult Cutthroat						
Biomass (g m ⁻²)	2.46	2.49	1.87	1.88	0.67	0.64
Number captured	38	40	33	39	11	14
Number PIT tagged	20	30	29	31	11	14
Absolute movement(m ^{-day})	0.3	0.1	0.5	0.1	0.3	0.1
Max movement (m)	44	22	72	25	42	23
Young-of-year (0+) Cutthroat						
Biomass (g m ⁻²)	0.02	0.04	0.08	0.04	0.06	0.03
Number captured	10	18	25	10	10	9

Abundance and Growth

The abundance and biomass of adult Cutthroat Trout were comparable in both 2013 and 2014, while in 2015, adult Cutthroat Trout abundance and biomass were reduced by nearly half compared to the previous 2 y. Lower abundances in 2015 may be indicative of lower survival rates prior to, and during, our study (Berger and Gresswell 2009), or by large-scale movements of individuals out of our study reaches prior to initial marking events in early August (Hubble 1992). We did not measure survival during our study, but numerous studies have found reduced over-winter survival (Søgard and others 2009; Alexiades and others 2012), as well as lower survival during low-flow events (Berger and Gresswell 2009; Grantham and others 2012).

Average growth rates of recaptured Cutthroat Trout were negative during all 3 summer seasons in both study reaches (fish lost weight on average). During summer, lower in-stream production rates and low discharge reduce overall prey availability for drift feeding fish (Boulton 2003; Wood and Armitage 2004; Power and others 2013). In addition, an overall reduction in wetted area during low-flow can concentrate fish and increase competition for food (Power and others 2013). Consequently, other studies evaluating salmonid growth also report reduced growth rates during low-flow conditions (Boughton and others 2007; Hayes and others 2008). As trout growth is often density dependent (Harvey and others 2005; Teichert and others 2010) the reduction in trout abundance in 2015 may have masked the full

magnitude of the drought conditions on growth because it may have allowed the remaining fish to grow (or, more specifically not lose weight) at rates similar to previous seasons despite lower stream discharge and a probable reduction in resource availability.

Movement Patterns

Multiple studies have documented the movement of salmonid species during the summer low-flow period with fish moving both upstream (Peterson 1982; Kahler and others 2001) and downstream (Young 1996; Schmetterling and Adams 2004). In 2013 and 2014, we found no outstanding trends in summer movement patterns, but in the year with unusually low discharge (2015) this changed; more fish stayed close to their original capture location and when individuals did move, it was upstream. One explanation for this reduction of movement is reduced connectivity due to impassable barriers such as low water or fully dewatered channel sections during extreme low flows (Kahler and others 2001). In cases where low flows create obstructions for fish, movement often occurs to refuge habitats near the edges of the passable habitat. For example, Brown Trout (*Salmo trutta*) in an intermittent stream in New Zealand preferentially moved upstream to seek refuge habitat due to seasonally impassable downstream barriers (Davey and Kelly 2007). Alternatively, fish could have moved downstream and fully out of our study reaches in 2015. Without complete (100%) recapture of marked individuals, movement out of the system remains a possibility, which would have been

undetected with the study design. While the majority of fish within a population are relatively sedentary, a subset of individuals typically have home ranges greater than the extent of our study reaches (Gowan and others 1994; Rodriguez 2002). We sampled 50 m downstream of the lower study reach and captured no individuals in 2015, and no individuals from Reach 1 were ever captured downstream in Reach 2 suggesting large downstream movements in 2015. The fact that we had our greatest recapture success in 2015 (76% of individuals were recaptured) lends further support to the explanation of reduced movement, under the assumption that capture efficiencies and mortality rates remained the same among study years.

We recaptured all of the Cutthroat Trout that moved from their release point in 2015 in pool habitats. Adult trout prefer pools and runs, particularly during low-flow conditions (Heggenes and others 1991; Kahler and others 2001), likely because these habitats minimize energetic costs associated with swimming (Fausch 1984), provide more cover (Berg and others 1998), and often are thermal refugia during low-flow events (Baird and Krueger 2003). While adults can be found in riffle habitats during summer (Armstrong and others 1998), their growth rates are highly reduced compared to trout occupying pool habitats (Rosenfeld and Boss 2001), and this result is generally consistent among studies examining summertime growth of trout (Boughton and others 2007; Hayes and others 2008). Thus drought can limit habitat availability, making pools desired low-flow habitats despite increased potential for agonistic and density-dependent interactions (Kahler and others 2001; Baird and Krueger 2003; Davey and others 2006).

We evaluated potential size-associated drivers of movement by comparing total length to movement of Cutthroat Trout. In stream dwelling salmonids, larger individuals tend to move greater distances relative to smaller individuals (Young 1994; Swanberg 1997; Bunnell and others 1998; Gowan and Fausch 2002). In our study system, we found no such relationship in any survey year within the constraints of our sampling design. However, we did not quantify movement patterns of juvenile Cutthroat Trout or individuals <70 mm, and the range of body lengths in our study stream was relatively narrow with few individuals exceeding 150

mm, making size-associated movement patterns difficult to identify. Larger fish may also be more susceptible to predation during low-flow conditions (Power 1987), so we cannot, from the data available, differentiate between movement and mortality for fish that were not recaptured. A study of age-0+ juvenile trout documented movement from lateral habitats to nearby pool habitats with increases in body size (Moore and Gregory 1988), but little is known about longitudinal movement as marking and recapturing individuals of this age class over large areas can be difficult.

When considering Reach 1 and Reach 2 individually, we found that the majority of individuals in Reach 2 stayed within the habitat unit in which they were initially released, whereas the majority of trout in Reach 1 moved to a different habitat unit. A likely explanation for this movement pattern is that the higher abundance of large wood and steeper gradient in Reach 2 allowed for greater abundance of pools compared to Reach 1, as well as an increase in step-pools in this reach. Therefore, pools in Reach 2 were often associated with a cascade-habitat feature that potentially affected movement. Whether due to more suitable habitat in the pools or restricted upstream movement, fish released into Reach 2 generally exhibited less summer movement than in Reach 1.

Conclusion

Summer stream flows in many mountainous landscapes across western North America are often associated with snowpack accumulated in the winter (Barnett and others 2005). Limited winter snowpack can reduce summer discharge and prolong the period of low-flow conditions, thereby causing a disturbance in montane streams (Difffenbaugh and others 2015). Cutthroat Trout populations declined by half during a drought year in the headwater stream ecosystem we studied, and individuals persisted by moving to pools during this time period. During the drought of 2015, we found that Cutthroat Trout moved preferentially to pool habitats in an upstream direction, while individuals showed no clear directional bias during the 2 non-drought years (2013, 2014). This highlights the use and importance of deep pool habitat as areas of refuge for this species during extreme events.

Fish in Reach 2 moved less than fish in Reach 1 overall, likely due to habitat availability, but this pattern was more pronounced during the 2015 drought.

With increased drought we may expect to see a reduction in the abundance and movement of fish in headwater streams. The response of fish growth (or mass loss) over summer will depend upon the responses in abundance given the density-dependent nature of fish growth in these systems. Overall, pool habitat is obviously important for stream fish in small headwater streams, and if climate change increases drought frequency and intensity in the Pacific Northwest, these habitats may become increasingly critical to fish survival. Features that promote the creation of deep and larger pool habitats, therefore, warrant particular focus in habitat assessments and in any restoration or conservation efforts devoted to headwater ecosystems.

ACKNOWLEDGEMENTS

We would like to thank K Pospisil, C Kopet, E Purvis, E Heaston, G Jones, and L Still for their assistance with field collection. Data and facilities were provided by the HJ Andrews Experimental Forest research program, funded by the National Science Foundation's Long-Term Ecological Research Program (DEB 1440409), US Forest Service, Pacific Northwest Research Station, and Oregon State University.

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Submitted 19 October 2017, accepted 13 August 2018. Corresponding Editor: Denim Jochimsen.