Article

# Species-Specific Abundance Response of Montane Stream Fishes to Drought-Induced Variation in Streamflow 

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#### Abstract

Climate change projections in the western United States suggest that snowpack levels and winter precipitation will decline, but mean annual precipitation levels will remain unchanged. Mountain streams that once saw a constant source of water from snowpack will begin to see large seasonal variation in flow. Increased stream intermittency will create significant conservation risks for fish species; however, few studies have examined the abundance responses of fish in high elevation streams to the shift from perennial to intermittent flow. To determine the effects of stream intermittency on fish abundance in a montane stream, we quantified changes in abundance for five species over a five-year period that exhibited extreme variation in streamflow. Responses varied by species and life stage, suggesting that the shift from perennial to intermittent flow will cause significant declines in abundance for some species. Northern leatherside chub may experience large decreases in their range as the availability of perennial streams decreases. The study of drought effects on fish abundance will be crucial to the conservation of biodiversity in montane regions of the world.


Keywords: drought; stream intermittency; climate change; northern leatherside chub

## 1. Introduction

Climate change projections in the western United States suggest that while mean precipitation levels are likely to be unchanged from historical values, snowpack levels and winter precipitation will decline [1-4]. Watersheds in the western United States, especially in mountainous regions, are strongly dependent on snowpack [5,6] to provide a constant source of runoff through the summer before new snow can accumulate in the colder months [7]. As a consequence of this decrease in winter precipitation (usually in the form of snow), typically perennial mountain streams will experience declining runoff and higher rates of stream intermittency [8-10] during the hot and dry summer months. Rising temperatures will also lead to earlier melting of the snowpack, thus diminishing water supply earlier in the year $[5,11]$ and leaving less for the hot summer months. As temperatures rise, precipitation will shift from a snow-based system to a more rain-dependent system and streams that once were fed by a constant source of water from snowpack will begin to exhibit large seasonal variation in flow [1,12] including periods of intermittent flow especially in summer months.

Populations of stream fishes are strongly affected by drought-induced declines in streamflow [13-15]. Stream fragmentation as a result of reduced flow during periods of drought leads to reduction in habitat variation, increased predation and competition, and reduced water quality [16,17]. Not surprisingly, fish abundances tend to decrease in periods of drought and increase in high precipitation periods [18]. Habitat fragmentation and reduced variability can result in reduced diversity and richness in stream fish assemblages [19,20]. Increased drought frequency as a result of climate change may create significant conservation risks for some fish species, and more stress-tolerant species may
benefit at the expense of less stress-tolerant species [21]. Some fish species are well adapted to variable streamflow, others respond poorly to hydrological boom and bust cycles [22]. Although effects of drought on fish abundances have been documented in several stream systems $[23,24]$, few studies have examined responses of fish in high elevation stream systems to the shift from perennial to intermittent flow.

To determine effects of drought-induced stream intermittency on fish in a montane stream, changes in abundance of species and life stages were quantified for five species over five years. The five years we monitored started with perennial streamflow, characteristic of past patterns, but were followed by three years of drought conditions such that the stream became intermittent in flow in two of the last three years. This was the first occurrence of intermittent flow in recent history at the study site. We document species and life stagespecific responses of abundance to this change in flow and suggest that the climatic shift from snow to rain will likely result in decreased richness and diversity in fish assemblages in high mountain streams.

## 2. Materials and Methods

### 2.1. Study System

We quantified the abundance of stream fishes in an upper segment of Yellow Creek, (located in southwestern Wyoming USA; $41^{\circ} 01^{\prime} 48.45^{\prime \prime} \mathrm{N} 110^{\circ} 58^{\prime} 24.08^{\prime \prime} \mathrm{W}, 2222$ m elevation). Yellow Creek is a tributary of the upper Bear River, and it originates in Utah and flows northward into southwest Wyoming (Figure 1). This section of Yellow Creek has had perennial (year-round) flow throughout the last several decades (personal communication, Kyle Lowham, landowner of the area where the sample segments were located). Middle and lower Yellow Creek has several diversions and has a history of being completely dewatered because of diversions of water for agriculture during the summer months. However, the stream in the study area exhibits a natural perennial flow regime driven mainly by snowmelt through the summer. Some evidence of recent erosion of the stream banks and downcutting exists, but it is not clear if this is a consequence of land use changes or normal processes driven by variation in climate. The stream in this area included the complete native assemblage of fishes for the area and no introduced fishes. Five species regularly occurred in the study site: Richardsonius balteatus, redside shiner; Lepidomeda copei, northern leatherside chub; Cottus bairdi, mottled sculpin; Rhinichthys osculus, speckled dace; and Catostomus platyrhynchus, mountain sucker. Onchorhynchus clarkii, cutthroat trout, are common above the study site but were only occasionally found in the study section. Richardsonius balteatus and L. copei are mid-water carnivores, C. bairdi is a benthic carnivore, $R$. osculus is a benthic omnivore, and C. platyrhynchus is a benthic herbivore [25]. All five species were represented by both juvenile and adult life stages in the samples.

### 2.2. Streamflow Characterization

The period of the study (2011-2015) encompassed high precipitation years followed by extreme drought years. Flow in Yellow Creek changed dramatically from high to low precipitation years. To characterize historic streamflow, we used a combination of historical stream gauge data. Unfortunately, there is no stream gauge on the upper section of Yellow Creek. One stream gauge on the middle section (USGS 10017000, 1962-1978) was only operational for a few years, and not during the study period. Thus, we used streamflow from the upper Bear River as a surrogate for streamflow in the study area on Yellow Creek. The stream gauge we used (USGS 10020300, located about 50 km away from study site) had 60 years of data on mean annual streamflow. To ensure that Yellow Creek flow could be accurately represented by Bear River flow we plotted Bear River flow and the available period of Yellow Creek flow on the same graph. Bear River flow is higher (it is a larger stream), but the pattern is very similar between the two systems (Figure 2). This similarity in flow is expected because both systems head in the same area of the northwestern Uinta mountains and flow somewhat parallel, northward until their confluence near the town of Evanston, Wyoming USA. Over the course of the study,
observed streamflow during the summer sampling period was as follows: 2011, moderate, but perennial flow; 2012, moderate, but perennial flow; 2013, non-flowing, isolated pools in the study area; 2014, low, but perennial flow; 2015, non-flowing, isolated pools in the study area. For our comparison to patterns of fish abundances we considered three years to be normal, year-round, perennial flow, 2011, 2012, and 2014; and two years to be intermittent flow, 2013 and 2015.


Figure 1. Map of study site and stream gauge locations. Insets and red star illustrate general location of study site in North America. Yellow Creek and the Bear River both originate in the Uinta Mountains of northern Utah and flow northward before their confluence near Evanston, Wyoming, USA (black star). Red dots indicate the sample site and the location of the Yellow Creek Gauge and the Bear River Gauge referenced in Figure 2.

### 2.3. Fish Population Abundance

To determine how this stream fish assemblage responded to variation in streamflow among years, we quantified abundances for each of the five species in the same section of Yellow Creek for five years (2011-2015). Sampling was done in mid-summer (late July to early August) every year, which is typically the driest part of the year with the lowest streamflow. To organize sampling and data collection, we divided the stream into 50 m segments. For the first year, five and a half 50 m segments were sampled in conjunction with a mark-recapture study. The final 75 m contained incomplete data on three of the fish species for the first year and was not used in the analysis for 2011. In subsequent years, we used all data from original segments and added contiguous downstream and upstream segments to increase annual sample sizes. Four to six downstream segments and four or five upstream segments were sampled in subsequent years, for a total of $600-800 \mathrm{~m}$ of the
stream (Figure 3). All five species in the study section have similar life histories in that they mature at the beginning of their second year of life. All species spawn in the spring (May to June), and young-of-year fish are not susceptible to electroshocking in this system during July and August when sampling occurs. Young-of-year fish are extremely small and are not reliably captured by our gear. Thus, one-year-old fish comprise the juvenile life stage, and they represent the fish produced in the previous summer. This creates a one-year time lag in our measure of juvenile abundance and recruitment.


Figure 2. Average daily discharge data for both Yellow Creek and the Bear River. Comparison of the data shows the association between the flow of both systems. No data were available for Yellow Creek within the years of our study; thus, the Bear River is used as proxy. Yellow Creek is represented by the dashed line and the Bear River by the solid line. Years with perennial flow are marked with a solid diamond and years with intermittent flow are marked by an open diamond. Scale for Yellow Creek is represented on the right and the Bear River on the left. Years within our study are highlighted with a gray background. Yellow Creek Gauge: USGS 10017000. Bear River Gauge: USGS 10020300. While Yellow Creek flow patterns have been quite variable, this stream has had perennial (year-round) flow over the past few decades (personal communication, Kyle Lowham); intermittence is a new phenomenon that occurred in 2013 and 2015 in the study section.


Figure 3. Stylized representation of the stream with sampling segments indicated by solid black lines. Each segment was 100 m in length and the width of the stream varied from two to five meters. Years that each segment was sampled are listed adjacent to the segment. The two segments in the middle labeled as "all years" represent the two original 100 m segments sampled first in 2011 and all years thereafter for the duration of the study. Additional segments were included in the two years with intermittent flow because some parts of all segments were dry.

To estimate the numbers of individuals for each species, we sampled using a backpack electroshocker with standard electrofishing procedures [26]. We used block nets to provide closure at the ends of the segment during years when the stream reach was flowing. We used a two-pass removal depletion method to estimate abundances within segments. After placing captured fish in aerated coolers filled with stream water, we identified fish to species and categorized them by life stage (juvenile or adult) based on standard length, and then returned the fish to the same section of stream. In 2011 (the first year), size data for R. balteatus were only available for the first 30 fish caught (sampling in 2011 was focused mainly on R. osculus, and L. copei, for a mark-recapture study that is reported elsewhere). However, we recorded the number captured of $R$. balteatus for each segment and pass of the stream reach. We calculated the ratio of adult to juvenile life stages of the first 30 fish and used that ratio to estimate the $R$. balteatus life stage distribution (adult or juvenile) for additional segments for 2011 only.

To estimate abundances, we used a maximum-likelihood population estimator [27]. To calculate valid abundance estimates from a two-pass removal method, a higher number of specimens must be captured in the first pass compared to the second pass because the estimator is based on sampling without replacement. For species with naturally low abundances, some segments contained higher second pass catches compared to first catch passes. To avoid the problem of increased catch in second passes, we combined two sequential 50 m segments to generate a 100 m segment. Sampling effort and methods were the same for any two 50 m segments, thus they could be considered as one continuous segment for data analysis. Combining segments in this way corrected all cases of increased second-pass catches for all species and life stages. We used these combined catch totals to estimate the abundance of each species and life stage and to calculate confidence intervals on the estimate. We sampled 200 m of the stream in the first year (2011) and $600-800 \mathrm{~m}$ in subsequent years (2012-2015). Thus, the numbers of 100 m segments we used in the analysis were $2,6,8,6$, and 7 , from 2011 to 2015, respectively, giving a total of 29 segments multiplied by five species and two life stages for a total sample of 290 abundance data points for analysis. Each segment was considered as a replicate of species-specific fish abundance estimates within each year.

### 2.4. Analysis

To determine how the abundances of fish varied across years, among species, and between juveniles and adults, we used a generalized linear model (SAS 9.2; Proc GENMOD, SAS Institute Inc., Cary, NC, USA). The response variable was abundance within a given 100 m segment, and predictor variables were species ( $L$. copei, R. osculus, R. balteatus, C. platyrhynchus, or C. bairdi), life stage (adult or juvenile), and the calendar year (2011-2015) as a surrogate for variation in flow (described above). Each model included two-way interactions and the three-way interaction of the fixed effects. Because abundances were essentially count data, we assumed a Poisson distribution, and the model included a log-link function.

## 3. Results

Two of the three main effects (with the exception of the life stage), all two-way interactions and the three-way interactions were significant predictors of fish abundance (Table 1). The significant three-way interaction suggests that the abundance of juveniles and adults varies among species across years. Patterns of abundance during this extreme drought event were species-specific, four of five species exhibited a pattern of higher abundance in perennial flow years of 2011 and 2012 and lower abundances, especially of adults, in the three following years of drought (2013-2015). The years 2013 and 2015 were the first years in several decades where this section of Yellow Creek became intermittent (Figure 4a-d). Three of the four species that declined during drought years exhibited substantial increases in juveniles in 2015 (R. osculus, R. balteatus, and C. bairdi; Figure 4b-d), and R. osculus and $R$. balteatus both showed increases in adults in 2015. Lepidomeda copei was the second
most abundant species during 2011 and 2012 (behind R. osculus and similar to R. balteatus) but declined to near zero by 2014 and contrary to the pattern in the other three species, showed no sign of recovery in juveniles or adults in 2015 (Figure 4a). The exception to the large changes in abundance in response to drought years was $C$. platyrhynchus, the least abundant species in the system. Their abundances were low and relatively unchanged across all five years for both juveniles and adults (Figure 4e).

Table 1. Effect of species, life stage, and calendar year on fish abundance from the generalized linear model. Interactions are indicated by a * between main effects.

| Source | DF | Chi-Square | Pr $>$ Chi-Sqr |
| :---: | :---: | :---: | :---: |
| Year | 4 | 195.76 | $<0.0001$ |
| Life stage | 1 | 0.65 | 0.4192 |
| Species | 4 | 423.72 | $<0.0001$ |
| Year * Life stage | 4 | 32.12 | $<0.0001$ |
| Year * Species | 16 | 1336.13 | $<0.0001$ |
| Species * Life stage | 4 | 326.62 | $<0.0001$ |
| Year * Species * Life stage | 16 | 378.19 | $<0.0001$ |



Figure 4. Cont.


Figure 4. Mean fish abundances by species per year for the five species in this study (a-e). Error bars are $95 \%$ confidence intervals of the mean. Adults are represented by the solid line and solid circles, and juveniles are represented by the dashed line and open circles.

## 4. Discussion

The response of stream fish to the shift from perennial to intermittent flow varied across the five species as has been observed in other ecosystems [28]. The most common response to the declining flow experienced from 2011-2013 (intermittent flow developed in 2013), was an extreme decline in abundance. All five species persisted at low levels during 2013 and 2014, and three of five exhibited strong increases in juvenile abundance in 2015. Interestingly, although in 2014 the stream exhibited perennial flow throughout the summer, in 2015 the stream exhibited intermittent flow much like during the summer of 2013. The substantial increase in juvenile abundance observed in R. osculus, R. balteatus, and C. bairdi suggests good recruitment of young-of-year during 2014 (a perennial flow year) that were then captured as juveniles in 2015. As noted above, juveniles in our study are one-year-old fish that were spawned in the previous year. Thus, although 2015 was another year of intermittent flow, we would expect the three species that showed large increases in juvenile numbers to persist through to subsequent years. In addition, two of three of these species showed substantial increases in adults in 2015 indicating good survival of juveniles and adults in 2014. These three species, exhibit a resilient response to drought-induced intermittency in streamflow. Similar responses have been documented in species that regularly experience intermittency [15,18,28,29].

In most intermittent stream systems, native fish spawn in the spring when water is most likely to be flowing [30,31]. Thus, during dry parts of the year, survival of all size classes may be affected [15], but it is unlikely that reproduction (i.e., spawning and hatching of eggs) itself is affected. All fish species in Yellow Creek are spring spawners, and similar to what has been shown in other intermittent systems, it is mainly survival rates that are negatively affected by the drying and subsequent intermittent stream conditions. Spring spawning can be seen as an adaptation to potential intermittency later in the year. Although
L. copei is a spring spawner it did not exhibit a resilient response to intermittency like the other species.

In contrast to the three species that exhibited resiliency to intermittent flow conditions, L. copei continued to decline in the study system and did not show evidence of any juvenile recruitment from 2013 to 2015. In 2014 and 2015 only a couple of northern leatherside chubs were found in the entire $600-700 \mathrm{~m}$ of the stream that we surveyed. For another study (reported elsewhere), we marked all L. copei and R. osculus with a unique elastomer mark. The few L. copei captured in 2014 and 2015 were not marked individuals that had persisted in the system, but rather they were unmarked and had presumably immigrated into the system from upstream.

From a conservation perspective, the loss of L. copei is concerning. Lepidomeda copei was described as a separate species from the closely related Lepidomeda aliciae in 2004, and its current distribution is limited to a small number of sites in the Great Basin (including the Bear River drainage) and upper Snake River [32]. It is listed as a Species of Greatest Conservation Need in Utah, USA [32]. Reasons for its declining geographical distribution have been difficult to ascertain. It has similar trophic and abiotic requirements as other stream fishes in the region [25,33], but it does not seem resilient to habitat degradation (such as intermittent flow), or the presence of introduced predators such as Salmo trutta, (brown trout). As intermittency of streamflow increases in high elevation systems, distribution of L. copei may decline even more.

The mechanisms that caused L . copei to decline without recovery (in contrast to other fish species in the Yellow Creek) are unclear. In streams, fish that recover from droughts tend to be tolerant to the high temperatures and low oxygen availability often present in isolated pools [17]. L. copei is relatively tolerant to high temperatures [34]. Its tolerance to low oxygen availability is unknown, though, given the harsh environment in which it evolved, it seems unlikely that it would be uniquely sensitive to low oxygen. In intermittent Mediterranean streams, fish reproduction is limited not by harsh abiotic conditions per se, but by reductions in macroinvertebrates, generating resource limitations for fish populations [35]. Adult $L$. copei are trophically similar to another midwater carnivore, R. balteatus [25], but R. balteatus exhibited a strong demographic recovery in 2015 in Yellow Creek. However, L. copei differs from $R$. balteatus in its response to the threat of predation, and possibly in response to low water [36]. L. copei tends to reduce activity rate and movement in response to the threat of predation; whereas, $R$. balteatus increases activity rate and movement [36]. It could be that $R$. balteatus responds with increased movement when streams begin to dry. Thus, being more likely to find deeper refuge pools and to be able to weather drought more successfully compared to $L$. copei. In addition, it is possible that $L$. copei are unable to compete for shared resources with $R$. balteatus during times of low resource abundance. We did not survey resource abundance, but this hypothesis should be examined in future studies.

The abundance of C. platyrhynchus was relatively constant throughout the five-year period despite variation in flow. This is consistent with another study that showed that density of C. platyrhynchus was not influenced by stream discharge [37]. However, this study did not compare the effects of intermittent versus perennial flow. In contrast, drought has been suggested as a high-risk factor for C. platyrhynchus conservation [38]. How streamflow affects C. platyrhynchus abundance may depend on the severity of the drought duration and location-specific conditions, but our data suggest that they are resilient to temporary loss of streamflow.

Changes in precipitation patterns driven by climate change in the mountainous portions of the western United States will likely lead to changes in the distribution and abundances of stream fishes. Adaptations that allow for high levels of recruitment and recolonization after drought will allow some fish species to continue to persist in high mountain streams while other species, like L. copei, will likely decline rapidly and become extinct in affected drainages. If other populations of high mountain stream fish behave similarly, we can expect geographic ranges of fish with poor ability to utilize and recolonize intermittent streams to decrease as stream intermittency becomes more common and
populations decline to extinction. Further study of drought effects on fish abundance will be crucial to the conservation of biodiversity in montane regions of the world.

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Informed Consent Statement: Not Applicable, the study did not involve human subjects.
Data Availability Statement: Data for stream gauges can be found on the USGS website. https:/ / waterdata.usgs.gov/nwis/nwis, accessed on 26 April 2022. Data for fish abundances is archived in Dryad Digital Repository as https:/ / doi.org/10.5061/dryad.pk0p2ngr, accessed on 26 April 2022.

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