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Response to Drought of a Stream Fish Assemblage in a

High Elevation Stream in the Intermountain West

Richard M. Simkins

A thesis submitted to the faculty of Brigham Young University in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Response to Drought of a Stream Fish Assemblage in a High Elevation Stream in the Intermountain West

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One of the most influential disturbances for stream fish assemblages is large-scale declines in flow caused by periods of drought. Although stream characteristics are known to influence the response of stream fishes to drought, we asked if ecological traits of stream fishes determine, in part, their population level response to drought. To test for ecological trait-based responses to drought in a stream fish assemblage, we quantified species abundances over a period of 5 years that represented a wet to dry period. We sampled stream fishes in Yellow Creek, Wyoming, USA, a high elevation stream dependent on snow-storage for most of its flow. There were five regularly occurring species in the study site: redside shiner (*Richardsonius* balteatus), northern leatherside chub (Lepidomeda copei), mottled sculpin (Cottus bairdi), speckled dace (Rhinichthys osculus), and mountain sucker (Catostomus platyrhynchus). We used size class, species, and drought measures as predictors of abundance. Mean Palmer drought severity index over the growing season from the previous year (one year lag) provided the best predictor of stream fish abundances. Four of five species showed strong declines in abundance in response to drought conditions (mountain sucker abundance was not affected), but ecological traits of species were not good predictors of the magnitude of response to drought. Northern leatherside chub are most vulnerable to local extirpation during times of severe drought. Overall, juveniles showed a greater decline in abundance than adults in response to drought. Climate models predict that mountain streams will experience changes in flow regime, which may exacerbate effects of drought. Low flow refuge habitat may need to be incorporated into stream restoration designs to help increase recolonization in streams, especially for stream fishes that are most vulnerable to local extirpation and that have low recolonization rates.

Keywords: variation in water flow, Palmer Drought Severity Index, abundance effects, speciesspecific response, western USA

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Introduction

One of the most influential disturbances for stream fish assemblages is large-scale declines in flow caused by periods of drought (Grossman et al. 1998, Kiernan and Moyle 2012, Niu and Knouft 2017). Effects of drought on stream fish abundance are mediated by characteristics of the stream (Rolls et al. 2016). Large streams and rivers have less variation in flow than smaller streams (Taylor et al. 2006). Flow rarely stops in times of drought in large streams, whereas small streams are more prone to flash floods and periods of surface no-flow. Droughts can cause decreases or increases in species abundances (Matthews and Marsh-Matthews 2003). Widespread drought can affect stream fish assemblages by decreasing connectivity, availability of refugia, and likelihood of recolonization during periods of increased connectivity caused by decreases in abundance (Adams and Warren 2005, Davey and Kelly 2007, Driver and Hoeinghaus 2016). Prolonged droughts can create stream systems that are less diverse and more homogenous in fish assemblage structure (Lawson and Johnston 2016). Several studies have addressed how the type of disturbance (Matthews et al. 2013, Lawson and Johnston 2016) or stream characteristics (Keaton et al. 2005, Beugly and Pyron 2010, Driver and Hoeinghaus 2016, Rolls et al. 2016) influence changes in stream fish assemblages because of drought, but few studies have focused on the characteristics of the stream fish assemblage as a determinant of response to drought. Can measurable ecological traits of stream fish, such as size, habitat requirements, or diet predict mechanisms of change in stream fish responses to drought? Or, is the response unrelated to the fish's ecological traits?

Stream fishes may differ in their response to drought because of their ecological attributes (Mouillot et al. 2013). Species characteristics such as trophic relationships, habitat requirements, and body size are likely predictors of response to drought. Similarities in diet

(Freitas et al. 2012) or habitat (Bain et al. 1988), have been shown to influence response to these changes caused by variable stream flow (Mouillot et al. 2013). Smaller, younger fish may be more susceptible to changes in climate than larger, older fish (Magalhães et al. 2007). Size plays a role in over-winter survival of fish (Quinn and Peterson 1996) and could also affect survival during other harsh conditions or disturbance events. Size may also vary as a response to decreased resources, or changes in temperature that affect the growth rates of fish (Moyle et al. 2004). In stream fish assemblages, adults and juveniles of the same species can occupy different niches (Moyle and Vondracek 1985, Billman et al. 2008), and may have different responses to drought for each size class and species. Each species could also respond differently to drought, independent of their ecological traits because of stochastic events. To understand changes in stream fish assemblages during drought requires a focus on 1) specific ecological traits that have been shown to be important in a species response to drought, and 2) how ecological traits relate to possible mechanisms which affect assemblage structure.

To test for ecological trait-based responses to drought in a stream fish assemblage, we quantified species abundances over a period of 5 years that represented a wet to dry period. We tested multiple representations of drought condition to determine which measure can best describe the response of stream fishes to drought. We characterized the stream fish assemblage using functional groups, size structure, and individual species to determine which traits are important in determining response in abundance to drought.

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Methods

Study System

We quantified abundance of five species of stream fishes in Yellow Creek, Wyoming USA (41° 01' 48.45" N 110° 58' 24.08" W, 2222 m elevation). Yellow Creek is a tributary of the upper Bear River that originates in Utah and flows northward into southwest Wyoming. The stream channel in the study area has not been intentionally altered or channelized and there are no water diversions upstream or in the study area. The stream section exhibits a natural 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 site includes the full native assemblage of fishes for the area and no introduced fishes. Five species regularly occur in the study site: redside shiner (*Richardsonius balteatus*), northern leatherside chub (*Lepidomeda copei*), mottled sculpin (*Cottus bairdi*), speckled dace (*Rhinichthys osculus*), and mountain sucker (*Catostomus platyrhynchus*). Cutthroat trout (*Onchorhynchus clarkii*) are common above the study site, but were only occasionally found in the study section.

The five species of fishes represent three functional groups; mid-water carnivores (redside shiner and northern leatherside chub), benthic carnivores (mottled sculpin and speckled dace), and a benthic herbivore (mountain sucker). All five species were represented by both juvenile and adult size classes in the samples.

Data Collection

To determine how stream fish assemblages respond to drought, we quantified abundances for each of the five species in the same section of Yellow Creek for 5 years (2011-2015). This

time period encompassed both high precipitation years and drought conditions. Flow in Yellow Creek changed dramatically from high to low precipitation years with only isolated pools present in the low-water years. To organize sampling and data collection, we divided the stream into 50 m segments. The first year, five and a half 50 m segments were sampled in conjunction with a mark-recapture study. The final 75 meters, which represent the third original stream segment, contained incomplete data on three of the fish species and was not used in the analysis (for the first year). In subsequent years we used all data from original segments and added downstream and upstream segments (to ensure recapture of the original marked population). Four to six downstream segments and either four or five upstream segments were sampled in subsequent years, for a total of 700-850 m of the stream reach sampled per year.

To determine species abundance, we sampled using a backpack electroshocker and standard electrofishing procedures (Meador et al. 1993). We used block nets at the downstream end of a section to provide closure of the segment during years when the stream reach was flowing. We used a two-pass removal depletion method to estimate abundances within segments. We placed captured fish in aerated coolers filled with stream water. We identified fish to species and categorized them by size group (juvenile or adult) based on standard length, and then returned the fish to the same section of stream. In 2011, size data for redside shiner were only available for the first 30 fish caught because sampling was focused on speckled dace and northern leatherside chub for the mark-recapture portion of the study. However, we recorded abundance for each segment and pass of the stream reach. We calculated the ratio of adult to juvenile of the first 30 fish and used the ratio to estimate the redside size distribution (adult or juvenile) for additional segments. No other years or species presented a similar problem in data collection.

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To estimate abundances, we used a maximum-likelihood population estimator (MicroFish 3.0, Van Deventer 1989), which assumes that all individuals in the same group have the same probability of capture. 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. Some segments, as is common when species are in lower abundances, contained higher second pass catches. To avoid the problem of increasing catch for less abundant species, we combined two 50 m segments to generate a 100 m segment by summing first and second pass abundances. Sampling effort and methods were the same for both 50 m segments and could be considered as one continuous segment for data analysis. Because we ended up combining segments, there were 8 possible sampling areas each year, and any data that did not fit into those 100 meter segments was not used (Table 1). Combining segments corrected all cases of increased second pass catches for all species and size classes. We used these combined catch totals to estimate the abundance of each species and size class and to calculate confidence intervals on the estimate.

Stream flow conditions changed yearly, but calendar year designation is not representative of drought intensity. To characterize drought accurately we obtained two representative measures. They were 1) an average of the Palmer Drought Severity Index (PDSI) from the months of May to September, which correlates well with stream flow (Dai et al. 2004), and 2) average snow pack accumulation estimate using SnoTel data from March to April. Abundance of species can respond to current or previous drought levels, so we tested PDSI and snowpack for both current year correlations and one-year lag correlations. We tested all possible combinations of drought measures in separate models to determine which measure, or measures, best fit changes of abundance in stream-fish as a response to drought. Analysis

To determine which drought measure best explained changes in abundance, we created 15 mixed models (SAS Institute Inc. 2015. JMP® 12 Documentation Library. Cary, NC: SAS Institute Inc.). We used population abundances as the response variable, and used a log_{10} (x + 1) transformation to satisfy normality assumptions and control for abundance estimates of zero. Fixed effects included 5 species categories (northern leatherside chub, speckled dace, redside shiner, mountain sucker, and mottled sculpin), crossed with 2 size categories (adult and juvenile), and all possible combinations of the four drought measures as covariates. In each model, we included two-way interactions of fixed effects, and fixed effects with covariates as well as three-way interactions between the two fixed effects and each covariate. We did not include interaction terms between covariates in any of the models. The model equation was:

Segment was included as a random effect to adjust for potential non-independence among linearly connected segments. We used model selection procedures based on AICc scores (Table 2; Johnson and Omland 2004) to choose the best drought measure(s) to predict changes in abundance.

We chose the best fitting model and then evaluated fixed effects and the covariate drought measure. Interaction terms including drought measure are representative of the response of the given term to drought conditions. We used Bonferroni corrected 95% confidence intervals of slopes from the species-drought measure interaction to determine if functional groups based on feeding methods and habitat preference were more similar in their response to drought, or if each species responded differently to drought conditions. Similarly, we compared the resulting slopes from the size class-drought measure interaction (a pairwise comparison between adult and juveniles), to determine if size classes responded differently to drought conditions.

Results

The model of fish abundance based on Palmer Drought Severity Index with a one-year lag (PDSI lag) as the only covariate had the lowest AICc score (Table 2). The Akaike weight for the model of PDSI lag was one, suggesting that in comparison to the other models, this model was the only probable representation. The PDSI lag model had an adjusted r^2 of 0.603. Thus, we used PDSI lag for the final model.

The three-way interaction of size, species, and PDSI Lag was not significant to the model, suggesting that sizes and species had uniform responses to drought. Species, PDSI lag, and all two-way interactions were significant in the abundance model of PDSI lag (Table 3). Species had different abundances in the stream and overall abundance in the stream was higher in wetter years than dry years. The size by species interaction shows that there was a difference in mean abundance among size classes and species, but was mainly driven by mountain sucker differences, and does not show response to drought.

The interaction between drought index score and size class demonstrates differing responses to drought between size classes of fishes (Table 3, Figure 1). Juveniles have a significantly higher slope in response to drought than adults, 0.094 compared to 0.059. Juvenile abundances are about 6 times higher in the wet years than the dry years of the study, whereas adult abundances only increase by half that amount, or 3 times higher in wet years compared to dry years. Juvenile abundances are lower than adults during drought and higher than adults during wet periods.

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The interaction between species and drought index had a significant effect on abundance in response to drought (Table 4, Figure 2). Groups of species that responded similarly to drought did not correspond to ecological trait-based functional groups (Table 4). Speckled dace had the highest slope (0.152) which was significantly different from all of the other species, except for northern leatherside chub. Speckled dace and northern leatherside chub had a decrease in abundance from the wettest to driest year of the study period of almost an order of magnitude (Figure 2). Northern leatherside chub, redside shiner, and mottled sculpin did not have significantly different responses. Mottled sculpin and redside shiner have a decrease in abundance of about half an order of magnitude from wettest to driest year of the study period (Figure 2). Mountain sucker had a slope that was not significantly different from zero, suggesting that there was no effect of drought on mountain sucker abundance.

Discussion

Changes in stream-fish abundance in response to drought corresponded to speciesspecific characteristics, and not ecological trait-based functional groups. Mottled sculpin and speckled dace shared similar habitat requirements (benthic habitat) and similar food requirements (carnivore and omnivore respectively), but did not share a similar response to drought conditions. Other studies found general trends in drought response based on food requirements (Freitas et al. 2012, Rios-Pulgarin et al. 2016), however in our system there was no evidence for a general food- or habitat-based response. Water column position has also been found to affect survival during drought. Midwater fish may be able to survive drought better because during droughts there are fewer flood events (Grossman et al. 1998). Water column position was not predictive of the response to drought in our system, because the lowest and highest responses to drought were both from benthic species of fish. Mountain sucker in the system present a special case. Mountain sucker have been shown to be affected by stream flow, and increased drought would increase the probability of their being extirpated from the system (Schultz and Bertrand 2012). However, mountain sucker are present at low levels every year. They may be able to recolonize quickly following a disturbance. The four most abundant species all exhibited a strong negative response in abundance to drought, similar to the response noted in other stream fishes (Davey and Kelly 2007, Bêche et al. 2009).

Size of fish was a general predictor in response to drought (Walters 2016), and juvenile fish of all species combined had a larger response to drought compared to adults. This is consistent with other studies that found adult fish were more resistant to drought than were juvenile fish (Schlosser 1985, Magalhães et al. 2007). Mortality rates differ between juvenile and adult fish (Lorenzen 2000), and this may explain some of the differences in response to drought we observed. Adult fish may be able to migrate better and thus have better access to refugia during drought than juvenile fish (Grossman et al. 2006). Adult fish also dominate more productive habitat areas which may make them energetically better able to survive droughtrelated resource limitation (Grossman et al. 2006). Adult fish survive better in colder temperatures (Quinn and Peterson 1996) whereas juvenile fish may be able to survive warmer temperatures (John 1964). Because the adult fish were more resistant to drought than the juvenile fish in our study, overwinter survival may be an important source of mortality during drought conditions. Older fish of a species survive better in drought conditions than do younger fish of the same species, but younger fish come back more quickly after drought periods. Reproductive success may be important and the best survivors of drought in this system may be the most fecund species. Adult fish may take time to rebound after a drought because their recovery is

based on recruitment; adult fish have to be juvenile fish first (Adams and Warren 2005). The quicker recovery in juveniles is consistent when looking at demography, the only way adult fish could have a larger response would be through massive migration of adult fish into the area. In a similar species, southern leatherside chub (*Lepidomeda aliciae*), a mark-recapture study showed that they rarely moved more than 50 m over the course of one year (Rasmussen and Belk 2012). Similarly, in good habitat, large-scale movements may not occur regularly in northern leatherside chub. Other species, including mottled sculpin, also show restricted movement in streams (Grossman et al. 2006, Rasmussen and Belk 2017), which may also limit recolonization in our system.

Species-specific response to drought may represent an evolutionary legacy effect for the stream fishes in our system. The pattern of loss from the stream reach can be represented by the individual responses, slopes, and starting abundance (i.e., the intercept) of each species. Both speckled dace and northern leatherside chub respond more strongly to drought, but it is northern leatherside chub that faces extirpation because of lower overall abundances. Speckled dace have a higher overall abundance than northern leatherside chub which helps them to withstand drought events. Northern leatherside chub are important components of stream systems. They are a biodiversity indicator species (Wesner et al. 2012), and their presence coincides with more complex trophic structure in streams (Wesner and Belk 2015). Loss of northern leatherside chub in response to drought may indicate a general collapse and simplification of the food web. It may be that northern leatherside chub are not well adapted to low flow conditions compared to other co-occurring species. It is interesting to note that northern leatherside chub have experienced a substantial decline in distribution (they are extirpated from greater than 50% of

previously occupied locations); whereas, none of the other four species have experienced similar declines in geographic distribution.

Both measures of drought based on the previous year's condition (PDSI or snow level) explained changes in abundance better than current measures. A delayed response in population because of disturbance effects is common in ecological studies (Stoffels et al. 2015, du Toit et al. 2016) and the amount of time to respond depends on organismal traits. Two processes can influence abundance 1) survival of current fish and 2) recruitment of juvenile fish. Current conditions affect direct mortality rates, i.e. if the conditions are unfavorable now, survival of an organism (John 1964, Woelfle-Erskine et al. 2017), reproductive success (John 1964, Hardie and Chilcott 2017), and growth potential (Quist and Guy 2001) are all affected. Mortality is affected by changes in the food availability for drift feeders (Matthews and Marsh-Matthews 2003, Love et al. 2008), possible increases in predation (Matthews and Marsh-Matthews 2003, Adams and Warren 2005), and less refuge availability (Davey and Kelly 2007). Past conditions are more indicative of recruitment from the previous year (Kiernan and Moyle 2012), i.e. if last year was a bad year, there will be lower abundances this year, but the size structure of the assemblage will be skewed towards older and larger individuals (Driver and Hoeinghaus 2016). Drought likely affects both current survival and recruitment of young in the next year. Because these stream fishes are relatively short-lived, recruitment may be manifest as a stronger effect and thus conditions from the prior year explain variation in abundance better than conditions in the current year. A reproductive response to disturbance requires time before it can be observed. Another explanation for the one-year lag is the sampling process. Young-of-year fish were not counted in the sampling thus juvenile fish would be a year old when sampled. It takes one year

for the fish to be counted in the sample which could account for the one-year lag model being a better predictor.

Climate change models suggest that in montane areas snow-storage systems are likely to change to rain-driven systems (Hamlet et al. 2005, Fritze et al. 2011). Snow-storage systems provide a slow melt during the summer such that stream flow can be maintained throughout the summer. On the other hand, rain driven systems are not based on storage, but flow only during wet periods. This change might dramatically alter drought dynamics in mountain streams such that even moderate droughts may produce large responses in flow. Precipitation shifts will lead to increased periods of drought, and increased possibility of no-flow conditions. The data suggest if no-flow events become more common, present stream fish communities in Yellow Creek may shift to be composed mostly of redside shiner and speckled dace. Under these conditions, stream habitat quality might be even more important to ensure adequate flow and appropriate temperatures for native species are present. Low flow refuge habitat may need to be incorporated into stream restoration designs to help increase recolonization in streams, especially for fishes that have low migration rates. These deeper than normal pools that are scattered in the stream system could not only provide refuge habitat during low flow years, but also create more frequent foci for recolonization during wet years.

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Table 1: Representation of sampling sites used during years. An "X" represents data was available for the given year of sampling. An "-" represents sections that were sampled partially, but not used in analysis.

	D3	D2	D1	01	02	03	U1	U2	U3
2011				Х	Х	-			
2012		Х	Х	Х	Х	Х	Х	-	
2013	Х	Х	Х	Х	Х	Х	Х	Х	-
2014		Х	Х	Х	Х	Х	Х	-	
2015		Х	Х	Х	Х	Х	х	Х	-

Table 2: AICc scores for models. All population models include: species, Size Class, Size Class* Species, Drought measure, Drought Measure * Species, Drought Measure *Size Class.

	AICc		
Model	AICc	Model Weight	Adjusted r ²
PDSI Lag	506.323	1.000	0.603
Snow Lag	529.399	0.000	0.552
PDSI, PDSI Lag	530.823	0.000	0.683
Snow, PDSI Lag	549.140	0.000	0.645
PDSI, Snow, PDSI Lag	549.220	0.000	0.748
PDSI Lag, Snow Lag	552.590	0.000	0.630
Snow	553.675	0.000	0.511
Snow, Snow Lag	557.984	0.000	0.620
PDSI	569.032	0.000	0.495
PDSI & Snow Lag	576.329	0.000	0.607
PDSI, PDSI Lag, Snow Lag	582.618	0.000	0.701
Snow, PDSI Lag, Snow Lag	587.117	0.000	0.684
PDSI, Snow	591.203	0.000	0.586
PDSI, Snow, PDSI Lag, Snow Lag	595.704	0.000	0.773
PDSI, Snow, Snow Lag	598.028	0.000	0.682

Table 3: Significance of fixed effects on model of abundance. Bolded numbers represent significant terms in the model.

Final Model - Effects Test						
Source	Nparm	DF	DenDF	F Ratio	Prob > F	
Species	4	4	262.6	59.5469	<0.0001	
Size	1	1	262.6	1.332	0.2495	
Size * Species	4	4	262.6	7.0453	<0.0001	
PDSI Lag	1	1	268.7	81.7634	<0.0001	
PDSI Lag * Species	4	4	262.6	9.8487	<0.0001	
PDSI Lag * Size	1	1	262.6	4.819	0.029	
PDSI Lag * Size * Species	4	4	262.6	0.3295	0.858	

Species Response to Drought					
Species	Slope	95% Confidence Interval			
Speckled Dace	0.152	0.085 to 0.219			
Northern Leatherside Chub	0.106	0.035 to 0.176			
Redside Shiner	0.075	0.016 to 0.133			
Mottled Sculpin	0.049	0.006 to 0.092			
Mountain Sucker	0.001	-0.055 to 0.056			

Table 4: Species slopes and 95% confidence intervals from the best model based on lag PDSI.

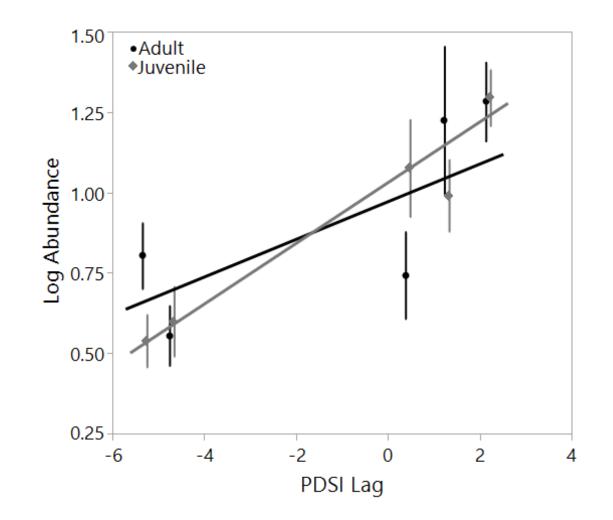


Figure 1: Graph of response of size groups to lag PDSI score. Mean abundance for each size group is represented. Error bars represent standard error.

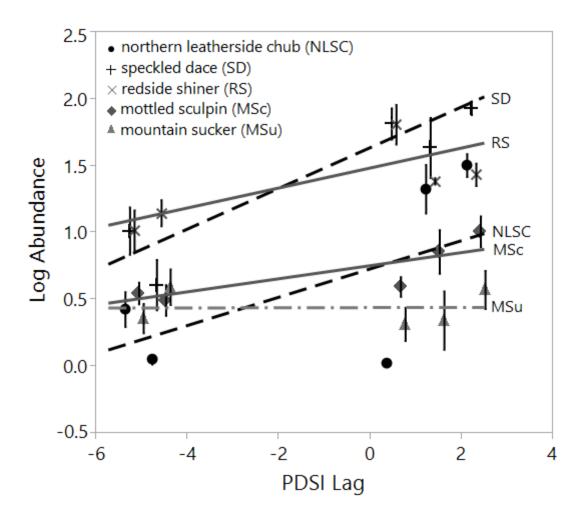


Figure 2: Graph of response of species abundance to mean PDSI lag score. Lines with same style show similarities in reaction to drought. Mean abundance for each species is represented. Error bars represent standard error.