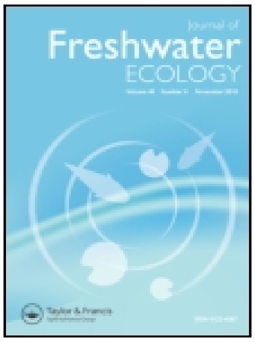

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Response of stream salamanders to experimental drought in the southern Appalachian Mountains, USA

Bryan Currinder[a], Kristen K. Cecala[a*,1], Robert M. Northington[b] and Michael E. Dorcas[a]

[a]*Department of Biology, Davidson College, Davidson, NC 28035, USA;* [b]*Climate Change Institute, University of Maine, Orono, ME 04469, USA*

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Droughts act as significant disturbances to freshwater animals and their ecosystems. Given the impending threat of more frequent and persistent droughts because of global climate change, the lack of data on the responses of many aquatic animals to drought is a cause for concern. This study examined the body condition of the most commonly detected species (*Desmognathus quadramaculatus*) and abundance of commonly found species after two years of experimental drought in two first-order streams in the southern Appalachian Mountains. Our results indicated negative effects of drought on the stream salamander community. The body condition of *D. quadramaculatus* larvae in experimental drought transects was significantly lower than larvae captured in control reaches, which may have resulted from lower macroinvertebrate production in experimental reaches. Additionally, larval *D. quadramaculatus* abundance declined 47% in experimental drought transects, and *Eurycea wilderae* larvae and *D. ocoee* adults were 70% less likely to be captured in experimental stream transects. Our findings contribute additional evidence that stream plethodontids have little resistance to drought. With extended droughts resulting from climate change more likely in the future, more research is necessary to determine if reduced body condition, production, and lowered abundance have effects on long-term population viability.

Keywords: amphibian; body condition; climate change; drought; ecological status; habitat management; stream

Introduction

Freshwater biota are susceptible to a variety of natural disturbances, and drought is one of the most significant (Lake 2003). Climate change is expected to alter the frequency and duration of droughts, with stream ecosystems expected to be vulnerable because precipitation largely drives stream flow (Hanson & Weltzin 2000). In the southeastern United States, models of climate change suggest little change in annual precipitation but instead predict changes in the timing and intensity of precipitation (Bates et al. 2008). This new trend could lead to extended periods of low discharge, especially during the summer (Bates et al. 2008; Wu et al. 2012). With a reduction or cessation of stream flow, more frequent and persistent droughts could disconnect streams, turning perennial streams into intermittent aquatic habitats (Boulton & Lake 1990; Stanley et al. 1997; Lake 2003; Magoulick & Kobza 2003). In the absence of surface flow, the downstream availability of items such as detritus, nutrients, and particulate matter may become increasingly limited

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[1] Present address: Department of Biology, University of the South, Sewanee, TN 37383, USA
*Corresponding author. Email: kkcecala@sewanee.edu

(Lake 2003; Northington 2013), and wastes and toxins may accumulate in disconnected pools (Lake 2003).

In the headwater stream ecosystems of eastern North America, salamanders of the family plethodontidae are often highly abundant and the dominant vertebrate predators (Davic & Welsh 2004; Peterman et al. 2008). Plethodontid salamanders can be indicators of habitat integrity in their respective ecosystems (Welsh & Droege 2001; Southerland et al. 2004; Welsh & Hodgson 2008; but see Kroll et al. 2009). The southern Appalachian Mountains are a global hotspot for plethodontid salamander diversity, but this diversity may become increasingly threatened by altered precipitation regimes as a result of global climate change (Bates et al. 2008; Milanovich et al. 2010). Even under the most liberal scenarios for increases in atmospheric CO_2, model projections by Milanovich et al. (2010) predict significant declines in suitable climatic habitat for southern Appalachian plethodontids before the end of this century, with increased occurrence and persistence of droughts expected to play a major role (Hanson & Weltzin 2000; Lake 2003; Malcolm et al. 2006; De Chazal & Rounsevell 2009).

A recent study has demonstrated the negative effects of supraseasonal droughts on the occupancy of stream-associated plethodontids, with larvae exhibiting limited resistance to drought (Price et al. 2012a). Despite the work of Price et al. (2012a) in the North Carolina Piedmont, there is little empirical evidence on the effects of drought on more diverse stream salamander communities in the southern Appalachian Mountains (Malcolm et al. 2006; Milanovich et al. 2010). Additionally, most studies on drought in stream ecosystems are opportunistic and cannot account for pre-drought conditions (Lake 2003). Studies implementing experimental drought circumvent these problems, making experimental drought an advantageous tool for assessing the effects of drought in the face of climate change (Northington 2013). Our objective was to determine if experimental drought negatively affected body condition and abundance of stream-associated plethodontid species in two headwater streams of the southern Appalachian Mountains. We hypothesized that salamanders would exhibit lower body condition and lower abundances in experimental drought transects relative to control transects.

Methods

Study species

Desmognathus aeneus, *D. quadramaculatus*, *D. monticola*, *D. ocoee*, and *Eurycea wilderae* (family plethodontidae) are stream-associated salamanders abundant in and along low-order streams throughout much of the southern Appalachian Mountains (Petranka 1998). These species are dominant members of headwater-stream communities but differ in their life history traits, making them good measures of production and ecosystem function (Peterman et al. 2008). Overall, studies of these species allow for a comparison of species that have different dependencies on water for both larval and adult life stages (Petranka 1998).

Data collection

Salamanders were surveyed in two perennial, first-order streams (watersheds 40 and 41) at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains during October 2012. A 30-m reach of each stream had experienced reduced annual base flow (experimental drought) for 25 months prior to sampling via a mean diversion of 50% of

Figure 1. Diversion method used to reduce stream base flow by 50% on average in the experimental drought transects. Baseflow was decreased from 0.24 to 0.10–0.16 L s^{-1} ha^{-1}.

the normal flow (additional details may be found in Northington 2013). The experimental drought transects were both located downstream of weirs that were subsequently blocked with plywood and drained via a drainage pipe to a point downstream from transects (Figure 1). Mean discharge for upstream sites were similar and averaged around 0.24 L s^{-1} ha^{-1}) whereas experimental drought transects varied between 0.10 and 0.16 L s^{-1} ha^{-1} (Northington 2013). All transects were similar in disturbance history, topography, drainage area, and experimental activities (Northington 2013).

To estimate abundance in both experimental drought and unaltered conditions, we designated two 30-m stream reaches on each first-order stream, one upstream of the diversion (control transect) and one within the diversion (experimental drought transect) located at least 50 m from one another. In each 30-m transect, we surveyed six 1-m^2 plots located 5 m apart. In each plot, we placed two 25 × 40 cm leaf-litter bags along the stream banks for a total of 12 leaf-litter bags per 30-m transect (see Jung et al. 2000). We assembled leaf-litter bags with 1 cm^2 plastic mesh and filled them with leaf litter from stream banks. After the leaf-litter bags had been set in the stream, they were left to soak for 24 h before we performed our sampling. We surveyed each plot for three consecutive days.

We sampled each transect by checking leaf-litter bags and thoroughly dip-netting and surveying beneath all cover objects within each plot. We checked leaf-litter bags by placing them in a bucket of stream water, gently agitating the trap to remove any salamanders, and then pouring the contents of the bucket through a dip-net. We identified species and stage (larvae or adult), measured snout-vent length (SVL) and total length (TL) noting any tail injuries, recorded each individual's mass, and returned each salamander to its capture plot. We removed leaf-litter bags after our final sampling occasion. To ensure sufficient sample sizes for body condition analyses, following the final day of sampling, we did additional active surveys to ensure that we captured and measured at least 15 *D. quadramaculatus* larvae from each transect. Individuals captured to meet this sample size were not included in our estimates of abundance.

Data analysis

D. quadramaculatus larvae were the only group captured in sufficient numbers ($n = 57$) to compare body condition between experimental drought and control transects. To obtain a body condition index, we used an ordinary least squared linear regression of log-transformed SVL and mass data for all individuals lacking tail injuries (Green 2001; Schulte-Hostedde et al. 2005). Further tests determined that no correlation existed between log SVL and the residuals of this regression, allowing us to use this relationship for further analyses ($r^2 < 0.001$; Green 2001). We tested whether the residuals between the expected and observed size-corrected masses were different between the control and experimental drought transects using an ANOVA in R (2.14.0; The R Foundation for Statistical Computing, Vienna, Austria) blocked by watershed (Sokal & Rohlf 1995).

To estimate the effects of experimental drought on salamander abundance, we used a binomial mixture model (Royle 2004) to estimate abundance from repeated counts of individuals from populations of unknown sizes (Royle & Nichols 2003; Royle & Dorazio 2008; Price et al. 2012b). We modeled abundance from the repeated count model using a Poisson regression that allowed abundance to vary by watershed (w) and by transect (t), permitting us to assess the relationship between experimental drought and abundance (λ_i). This formula is depicted by: $\log(\lambda_i) = \beta_{ws} + \beta_3 x_i$, where x_i represents the treatment. We modeled individual-based capture probabilities for each day and transect (p_{ij}) using a logit model that allowed capture probabilities to vary by day. This formula is depicted by: $\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 \times x_{ij}$, where x_{ij} represents the date of sampling for each site.

Abundance and capture parameters were evaluated for larval *D. quadramaculatus* using Bayesian inference via Markov-chain Monte Carlo methods (MCMC) in WinBUGS Version 1.4 (Spiegelhalter et al. 2003) with data handling in R (add-in library R2WinBUGS). MCMC uses iterative sampling from a simulated Markov chain to approximate estimates and dispersion of joint probability distributions such as the unknown relationship between abundance and capture probability. Visual inspection of Markov chains suggested that convergence was reached after 60,000 samples, which was then used as the burn-in period and all of those values were discarded (Kery 2008). Thereafter, every third value of 600,000 iterations was used to reduce autocorrelation between iterations resulting in the use of 180,000 iterations for inference about our parameters. Non-informative priors were used for all the parameters to result in normal distributions of each parameter. We calculated means, standard deviations, and the 95% Bayesian credible intervals represented by the values between 2.5 and 97.5 percentiles of the simulations.

Results

We captured 87 larval, juvenile, and adult salamanders of five species during our leaf-litter trap surveys. Most captures were *D. quadramaculatus*, with a total of 71 individuals (57 larvae and 14 adults). The remaining captures were as follows: seven *E. wilderae*, six

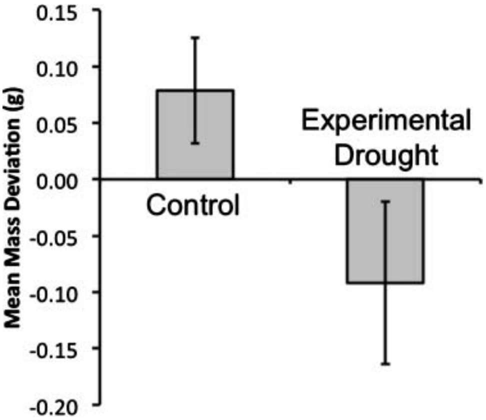

Figure 2. Mean mass deviation (±standard error) from the derived relationship between SVL and total mass of larval black-bellied (*Desmognathus quadramaculatus*) salamanders. Larval salamanders from the experimental drought transects were 13.9% smaller than those collected from the control transects in streams at the Coweeta Hydrologic Laboratory ($F = 4.14$, $df = 1{,}62$, $p = 0.046$).

D. ocoee, two *D. monticola*, and one *D. aeneus*. *E. wilderae*, and *D. ocoee* were 3.3 times more abundant in the control transects, and *D. monticola* and *D. aeneus* were found only within the control transects.

Body condition of *D. quadramaculatus* larvae was lower in the section of the stream experiencing experimental drought (Figure 2). Captured individuals from the experimental drought transects were 13.9% smaller for their SVL than individuals from control transects ($n > 15$ per transect; $F = 4.14$, $df = 1{,}62$, $p = 0.046$; Figure 2).

Abundance of larval *D. quadramaculatus* varied between watersheds, with watershed 40 having higher abundance in both transects relative to watershed 41. Larval *D. quadramaculatus* abundance was 1.9 times higher within the control transects relative to the experimental drought transects (Figure 3). Although the 95% credible interval of the parameter estimate of the effect of experimental drought spans zero (estimate: −0.45; Bayesian 95% credible interval: −1.19 to 0.27), because 81% of the distribution is negative, we may conclude that experimental drought likely has a negative effect on *D. quadramaculatus* abundance in streams at the Coweeta Hydrologic Laboratory.

Discussion

We used assessments of body condition and abundance to examine the effects of two years of experimental drought on stream salamanders in the southern Appalachian Mountains. Our results indicated that for larval *D. quadramaculatus*, body mass and abundance in experimental drought transects were significantly lower than in control transects. Additionally, *D. quadramaculatus*, *D. ocoee*, and *E. wilderae* captures each indicated that these species were more abundant within control transects than in experimental drought transects.

Our results of decreased body condition during experimental drought are consistent with previous findings that salamanders demonstrate negative responses to supraseasonal drought (Price et al. 2012a). Sustained free-flowing water is likely to play a critical role in maintaining *D. quadramaculatus* larval body condition, particularly when conditions of reduced baseflow are maintained over multiple seasons as they were in our study.

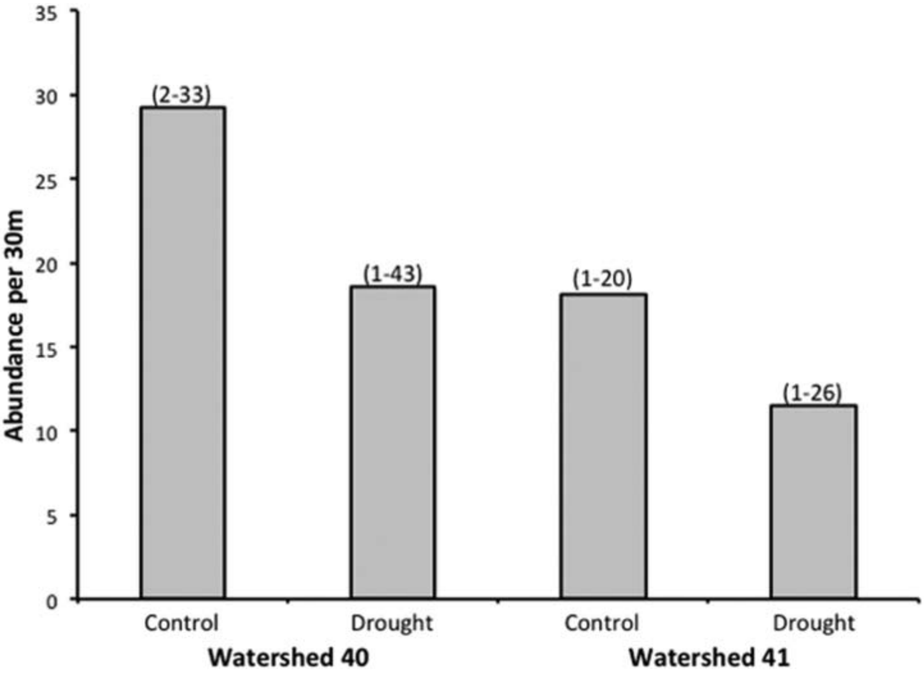

Figure 3. Larval *D. quadramaculatus* abundance was 1.9 times lower in 30-m experimental drought transects than in control transects with no hydrologic alteration in streams at the Coweeta Hydrologic Laboratory (effect of drought treatment = −0.45; 95% credible interval: −1.19 to 0.27). Abundance estimates of larval *D. quadramaculatus* obtained from our repeated count model were extrapolated to represent abundance throughout the 30-m transects. The Bayesian 95% credible intervals are indicated above each bar.

Reduced baseflow can decrease the transport and distribution of detritus and other nutrients downstream (Lake 2003; Steward et al. 2012), making it likely that our experimental drought transects were resource-deficient relative to control transects with unaltered base flow (Northington 2013). As predators of invertebrate detritivores, plethodontid stream salamander populations may be limited by the production of macroinvertebrates dependent on detritus (Wallace et al. 1997; Wallace et al. 1999; Johnson & Wallace 2005).

Stream drying has been shown to increase competition between larval stream salamanders, particularly for prey items (Petranka & Sih 1986). Invertebrate prey items declined in experimental drought transects relative to control transects (Northington 2013), heightening the potential for competition between *D. quadramaculatus* larvae in experimental drought transects (Petranka & Sih 1986). Reduced body condition due to reduced prey resources may have also been exacerbated by larval competition for refuge (Petranka & Sih 1986). Both food and spatial resources may limit body condition and also abundance of stream salamanders.

As lungless ectotherms with highly permeable skin, plethodontid salamanders are very susceptible to desiccation, particularly during times of drought (Keen 1984). Therefore, reduced baseflow under experimental drought may have reduced suitable habitat area and activity of *D. quadramaculatus* larvae. Although *D. quadramaculatus* adults are found in or near flowing water, *D. quadramaculatus* larvae typically take refuge beneath rocks or other debris in regions of fast-flowing water (Petranka 1998; Cecala 2012). Because drought reduces baseflow, the area of fast flowing water suitable for *D. quadramaculatus* larvae may have become limiting.

As we hypothesized, we captured fewer individuals and less diversity within the experimental drought transects than in the control transects. Our study was a rapid assessment of differences between experimental drought and control transects. Therefore, we had low sample sizes, particularly for *D. ocoee* and *E. wilderae*, and observed species over a short temporal scale. Studies with longer temporal scales and larger reaches may be necessary to elucidate the long-term relationship between drought and salamander abundance.

Adults and/or larvae may resist low-flow conditions by using both between-generation and within-generation refugium-use strategies (Lake 2003; Price et al. 2012a). Within-generation refugium-use strategies include temporary emigration to high-humidity or underground refuges, with high individual survivorship for stream salamanders occupying these refuges during drought (Griffith & Perry 1993; Feral et al. 2005; Price et al. 2012a). Between-generation strategies include complex life cycles that enable adult plethodontids to persist in times of drought because the high survivorship of one life stage can buffer the low survivorship of another life stage (Boulton 2003; Lake 2003; Price et al. 2012a). However, between-generation strategies may not have taken effect under only two years of experimental drought, highlighting the need for longer term study of these dynamics.

Our study provides insights into how climate change may affect stream salamander populations. Models of climate change predict more frequent and persistent droughts in the southeastern United States (Bates et al. 2008), with freshwater ecosystems like streams particularly vulnerable because they depend on balances of precipitation and evaporation (Schindler 1997). We observed that the body condition and abundance of *D. quadramaculatus* larvae was lower in transects experiencing experimental drought for over two years. More prolonged studies are needed to document whether these changes will negatively alter long-term population persistence in the face of more frequent and extended droughts in the future.

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