12-2020

The Effects of Multiple Stressors on Stream Communities: The Convergence of Drought, Nutrient Pollution, and Invasive Species

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Citation

Fournier, R. J. (2020). The Effects of Multiple Stressors on Stream Communities: The Convergence of Drought, Nutrient Pollution, and Invasive Species. *Theses and Dissertations* Retrieved from https://scholarworks.uark.edu/etd/3849

The Effects of Multiple Stressors on Stream Communities: The Convergence of Drought, Nutrient Pollution, and Invasive Species

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

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December 2020
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This dissertation is approved for recommendation to the Graduate Council.

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Abstract

Freshwater systems experience multi-faceted degradation from a variety of ecological and environmental stressors. Three common stressors in these systems, drought, nutrient pollution, and invasive species, have wide-ranging effects on stream population- community- and ecosystem dynamics. We have a broad understanding of how each of these stressors works to influence stream systems independently. However, we still know relatively little about if, and how, these stressors might interact when they co-occur. Though drought is a natural part of many stream systems, all three of these stressors can be exacerbated or facilitated by anthropogenic actions. Accordingly, as human population and resource use continue to grow, it becomes increasingly likely that these stressors will co-occur. To address this, I undertook research that sought to better explore the effects of multiple, simultaneous stressors on stream ecosystems. Here, I performed a series of manipulative experiments and constructed mathematical models that examined the effects of varying combinations of drought, nutrients, and invasive species along several ecological scales. I found that each of these stressors can impact stream ecosystems in diverse ways. For instance, drought negatively impacted many portions of the community, while nutrients caused bottom-up trophic effects. Additionally, my models indicated that both drought and invasive species can increase terminal extinction risk for fish metapopulations. However, I also observed several interactive effects. Drought and nutrient pollution interacted both additively and antagonistically on various portions of the food web simultaneously in my experiments, and drought and invasive species interacted synergistically to increase terminal extinction risk in my metapopulation models. Across all examinations, I found that the effects of both individual and multiple stressors are context dependent. Trophic role, life history strategy, and physical habitat all shaped stressor response. This work highlights the complexity of multiple stressors in stream systems and emphasizes a growing need to undertake additional examinations across various taxonomic groups and ecological scales. Our broad knowledge of the effects of individual stressors might not translate to multi-stressor

systems, and conservation and management plans that only account for individual stressors might be inadequate to protect resources in systems facing multiple stressors.

Acknowledgements

Science is never done in a vacuum (except astrophysics, I suppose), and this work was no different. First among the people I would like to thank is my advisor, Dan Magoulick. His patience, kindness, and wisdom made my entire research process possible. I would also like to extend my thanks to the rest of my committee: Michelle Evans-White, J.D. Willson, and Thad Scott for their material and immaterial support. I would also like to thank the administrative personnel of the Biology Department and the Cooperative Fish and Wildlife Research Unit: Becky Harris, Jan Warren, and especially Diane Moler.

Throughout this program, my labmates have been a constant source of encouragement, support, and biting sarcasm. To that end, I would like to thank Dustin Lynch, Chris Middaugh, Lindsey Bruckerhoff, Nicki Graham, Allyson Yarra, Brittany Fuller, Kayleigh Smith, Adrienne Ingram, Sarah Sorensen, Tyler Fox, and Leah Bayer. I would also like to thank the REU students, undergraduates, and technicians in the lab, especially Nathan Quimbo, Amber Maner, and Cherokee Gott.

I have been lucky to have support outside of my lab as well. Many members of the Evans-White lab, including: Brad Austin, Allyn Dodd, Kayla Sayre, and Sam Dias helped me fumble through bench work. Other members of the Coop unit, including: Auriel Fournier, Cari Seabright, John Herbert, and Joe Moore selflessly sacrificed their time, and their backs to shovel gravel with me. I would also like to thank Daniel Winfree who, in a testament to his saintly nature, drove to a remote Oklahoma field station when no one else was available to help me wrap an experiment. I am still not sure why.

Finally, I would like to thank my family. Their unwavering love and keen ability to not constantly ask “when are you going to finish” has kept me sane throughout the ups and downs

of this degree. I only regret that not everyone who started this journey with me was able to see the finished results.

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List of Published Papers

Chapter 3: Fournier, R.J., Bond, N.R., Magoulick, D.D., (2020). Modeling effects of disturbance across life history strategies of stream fishes. In press at *Oecologia*.

Introduction

Ecological degradation represents a severe threat to global biodiversity and anthropogenic actions can directly impact ecosystem structure and functioning (Benke 1990, IPBES 2019). Freshwater systems can be highly impacted by a wide variety of ecological stressors—including many that are anthropogenically-mediated (Jelks et al. 2008). Three of the most detrimental ecological disturbances to stream systems—drought, nutrient pollution, and invasive species—have diverse impacts on stream communities and are often some of the most pervasive threats to fauna in these systems. As human population growth and resource use continues to grow, the impact of these stressors is expected to increase through time (IPBES 2019). Additionally, it is increasingly likely that these stressors could co-occur and impact freshwater systems simultaneously (Omerod et al. 2010). Accordingly, a better understanding of the ecology of multiple-stressor systems is necessary to protect freshwater biodiversity.

Drought is a natural phenomenon in aquatic ecosystems with global influence that can greatly influence stream population and community dynamics (Townsend and Hildrew 1994, Beche et al. 2009). During drought, aquatic systems undergo several physical, chemical, and hydrological changes that can elicit direct biological responses (Lake 2003). To persist through drought, organisms must make use of the remaining—often limited—persistent waters (Magoulick and Kobza 2003). While confined to refuge habitats during droughts, relative density often increases, amplifying the strength of biotic interactions and leaving them susceptible to additional disturbances (Magoulick and Kobza 2003). Though drought is a natural phenomenon, anthropogenic activities can influence drought length and intensity (Bond et al. 2008, Marvel et al. 2019). Furthermore, anthropogenic climate change is expected to alter the frequency, magnitude, and duration of drought events (Bond et al. 2008). Drying constitutes a significant stressor to fish (Magoulick and Kobza 2003), invertebrate (Finn 2009), and algal (Thomas et al.

2000) populations; however, many species evolved adaptations to help them persist in drought-prone systems (Magoulick and Kobza 2003, Hodges and Magoulick 2011, Brasil et al 2013).

Nutrient pollution is one of the most severe threats to global freshwater biodiversity (Howarth and Marino 2006) and is often the most pervasive type of pollution present in aquatic systems (Mulholland et al. 2008). Excessive input of inorganic nutrients can have bottom-up trophic effects on stream ecosystems as algal and microbial communities can be limited in their growth by available nitrogen and/or phosphorous (Schindler 1977, Pringle 1990). At extreme levels, unchecked growth of primary producers can decouple trophic relationships and destabilize food web dynamics (Woodward et al. 2012). Additionally, nutrients can directly stimulate bacterial and fungal species, altering ecosystem functioning by influencing decomposition rates and secondary production (Hall and Meyer 1998, Tank et al. 2010). Under eutrophic conditions, dissolved oxygen levels can be greatly diminished during respiratory cycles—resulting in fish kills (Gilbert et al. 2002).

Invasive species can have detrimental impacts on stream ecosystems (Grabowska et al. 2010). Invaders can displace native species and have been implicated in the decline of native populations in a variety of aquatic systems (e.g., Windfield et al. 2011). Often, invaders directly compete with their native counterparts for resources (Sax et al. 2005). However, invaders can also influence native populations by niche displacement, introgression, hybridization, predation, as well as causing local or regional extinction (Mooney and Cleland 2001). The environmental and ecological damage caused by invasive species costs several billion dollars annually in the United States (Pimentel et al. 2005). Furthermore, both the relative effect of invaders (Rahel and Olden 2008), as well as the rates of introduction of new invasives (Huang et al. 2011) are expected to increase due to anthropogenic climate change.

Recent work has highlighted a need for increased scientific focus on multi-stressor systems (Omerod et al. 2010). The inherent heterogeneity of freshwater systems coupled with many environmental disturbances make them particularly vulnerable to multiple stressors (Omerod et al. 2010). Examinations of multiple stressors in freshwater systems are largely experimental and focus on population-level responses (Jackson et al. 2016). Population variables are more likely to display additive or synergistic responses to multiple stressors than metrics that explain community or ecosystem-level processes (Jackson et al. 2016). Despite the prevalence of multiple stressor problems in the management of freshwater systems, studies that explicitly seek to describe ecological responses to multiple stressors remain rare (Omerod et al. 2010, Reid et al. 2019). Because freshwater systems are susceptible to multi-stressor ecological degradation, and this vulnerability is expected to increase as human population and resource use grows (Strayer and Dudgeon 2010), more work must be done to disentangle the effects of multiple stressors in streams.

During periods of drought, individuals that seek refuge in persistent waters might see density-dependent increases in the effects of competitive or predatory relationships brought on by an invasive species (Matthews 1998). Furthermore, invasive species might be more able to deal with disturbances than their native counterpart, and drought events might facilitate additional invasions (Scoppetone et al. 2005). The extreme physical characteristics experienced during drought (e.g., spikes in temperature, dissolved oxygen levels), might amplify eutrophic effects brought on by nutrient pollution. However, drought might also mitigate the effects of nutrient pollution on primary production if grazer density is sufficiently increased during drought conditions (Welch et al. 1997), or if trophic cascades brought on by drought facilitate grazer release (Power et al. 1988).

While drought, nutrient pollution, and invasive species represent substantial disturbances to stream ecosystems, life history strategy can be an important predictor of how a species will respond to disturbance events (Van Winkle et al. 1993). To that end, Winemiller and Rose (1992) classified North American freshwater fishes into categories along a triangular continuum based on life history traits. Within this framework, generalized life history strategies represent a template for how a species might deal with a given disturbance event (Van Winkle et al. 1993). Accordingly, these templates can be used to examine population dynamics of fish species in a generalizable manner when more species-specific examinations are infeasible. Because life history mediates how biota respond to individual disturbances, a better understanding of how disturbances influence population dynamics of species with different life history strategies is fundamental to improving our capacity to predict the impacts of both individual and multiple stressors.

Because multiple stressors represent an increasingly prevalent ecological issue in freshwater systems, more research must be done to disentangle the effects of stressors across multiple geographic, temporal, and organizational scales. Accordingly, I sought to explore the issue of multiple stressors on Ozark stream communities. Broadly, this research attempted to address the following questions: *1) How do the individual effects of drought, nutrient pollution, and invasive species effect stream ecosystem dynamics? 2) How does life history strategy of fishes affect stressor response at the metapopulation level 3) Do stressors interact either synergistically or antagonistically to affect stream ecosystem structure and functioning?* To address these questions, I used a multi-faceted approach of mesocosm experiments and mathematical modeling to explore the ecological dynamics of streams that face varying combinations of drought, nutrient pollution, and biological invasion.

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Chapter 1: Drought and nutrient pollution produce both additive and antagonistic effects in stream ecosystems

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Running head:

Multiple stressors in stream ecosystems

Keywords:

Community dynamics, multiple stressors, stressor interactions, ecosystem functioning, trophic interactions

Abstract

1) Drought and nutrient pollution can affect the dynamics of stream ecosystems in diverse ways. While the individual effects of both stressors are broadly examined in the literature, we still know relatively little about if and how these stressors interact.

2) Here, we performed a mesocosm experiment that explores the compounded effects of seasonal drought via water withdrawals and nutrient pollution (1.0 mg/L of N and 0.1 mg/L of P) on a subset of Ozark stream community fauna and ecosystem processes. We observed biological responses to individual stressors as well as both additive and antagonistic stressor interactions.

3) We found that drying negatively affected periphyton assemblages, macroinvertebrate colonization, and leaf litter decomposition in shallow habitats. However, in deep habitats, increased sunlight penetration and drought-based concentration effects caused trophic cascades that released algal communities from grazing pressures; while nutrient enrichment caused bottom-up cascades that influenced periphyton variables and crayfish growth rates. Finally, the combined effects of drought and nutrient enrichment interacted antagonistically to increase survival in longear sunfish; and stressors acted synergistically on grazers causing a trophic cascade that increased periphyton variables.

4) Because stressors can differentially impact biota—and that the same stressor pairing can act both additively and antagonistically on different portions of the community simultaneously—our broad understanding of individual stressors might not adequately inform our knowledge of multi-stressor systems.

Introduction

Biodiversity is declining at an unprecedented rate (IPBES 2019) with broad impacts to ecosystem functioning (Worm et al. 2006). This decline is pronounced in aquatic systems, and freshwater biota are among the most threatened globally (Jenkins 2003). In stream systems, anthropogenic actions have exacerbated biodiversity loss, and systems in North America are especially threatened (Jelks et al. 2008, Dudgeon 2019). Two major stressors of these systems, drought and nutrient pollution, can impose a diverse array of ecological effects on stream communities. While both stressors are broadly examined in the existing literature (e.g., Magoulick and Kobza 2003, Woodward et al. 2012), studies that examine their combined effects remain relatively rare (but see Jackson et al. 2016). Stressor interactions are often complex as they can act additive, synergistically, or antagonistically (Folt et al.1999) and initiate regime shifts if ecological degradation is sufficiently high (Christiansen et al. 2006, Paine et al. 1998).

Freshwater systems are particularly vulnerable to the effects of multiple stressors because their inherent heterogeneity couples with a variety of disturbance events (Ormerod et al. 2010). Most examinations of multiple stressors are experimental in nature and focus largely on population-level responses (Jackson et al. 2018). Approximately 41% of documented stressor interactions in freshwater systems are antagonistic and may not affect diversity or functioning metrics, while stressor interactions that produce synergistic or additive effects account for 28% and 16% of studies, respectively (Jackson et al. 2018). Additionally, population variables are more likely to display additive or synergistic responses to multiple stressors than metrics that explain community or ecosystem-level processes (Jackson et al. 2018). Because freshwater systems are susceptible to ecological degradation brought on by multiple stressors, and this vulnerability is expected to increase as human population and resource use grows

(Strayer and Dudgeon 2010), more work must be done to disentangle the effects of multiple stressors in stream ecosystems (Christiansen et al. 2006).

Drought affects aquatic ecosystems on every continent and can greatly influence stream population and community dynamics (Townsend and Hildrew 1994, Beche et al. 2009). In addition to direct mortality brought on by drought, aquatic ecosystems undergo several physical, chemical, and hydrological changes during drying that can elicit direct biological responses (Lake 2003). During droughts, aquatic species must make use of refuge habitats in persistent waters or perish (Magoulick and Kobza 2003). In systems like the Ozark Highlands of Arkansas, Missouri, and Oklahoma, streams tend to dry in the late summer and early fall (Hodges and Magoulick 2011). Unlike press-style supraseasonal droughts, seasonal droughts in these systems tend to pulse their effects in a relatively short period of time before returning to normal flow conditions (Gasith and Resh 1999). The riffle-pool geomorphology of these streams, allows pools to remain watered during seasonal drying events and serve as refuges (Davey and Kelly 2007; Dekar and Magoulick 2007). However, the density of organisms increases when they are confined to refuges, amplifying the relative strength of biotic interactions and leaving them susceptible to additional disturbances (Lake 2003). While drying constitutes a significant stressor to fish (Magoulick and Kobza 2003), invertebrate (Finn 2009), and algal (Thomas et al. 2001) populations, many species evolved adaptations to help them persist in drought-prone systems (Magoulick and Kobza 2003, Lake 2003, Bond et al 2008, Hodges and Magoulick 2011, Brasil et al 2013).

Nutrient enrichment represents one of the most severe threats to global freshwater biodiversity (Howarth et al. 2000) and is often the single greatest category of pollution in aquatic systems (Mulholland et al. 2008). Anthropogenic input of inorganic nutrients via agriculture, urbanization, or the burning of fossil fuels can have bottom-up trophic effects on stream ecosystems as algal and microbial communities can be limited in their growth by available nitrogen and/or phosphorous (Schindler 1977, Pringle 1990). In lower order streams, benthic algae are often the primary drivers of autochthonous primary production (Vannote et al. 1980). When algal growth is not nutrient-limited, water quality can be diminished via decreased dissolved oxygen levels (resulting in fish kills) or algal-mediated toxins (Leflaive 2007). Under extreme levels of pollution, an overabundance of algal biomass can decouple trophic relationships and destabilize food web dynamics (Tank and Dodds 2003). Nutrient enrichment can also directly stimulate bacterial and fungal growth, increasing detrital decomposition rates and secondary production (Hall and Meyer 1998, Tank et al. 2010, Rosemond et al. 2015). Additionally, if systems are enriched over long time scales, communities might become increasingly homogenized across local (α diversity) and regional (β diversity) scales with corresponding ecological and evolutionary consequences (Donohue et al. 2009).

While both drought and nutrient pollution can influence stream ecosystem dynamics individually, these stressors might interact in ecologically meaningful ways. As water levels decrease throughout a system, habitats are more prone to extreme physical environmental conditions including spikes in temperature and dissolved oxygen levels (Matthews 1998). During normal conditions, churning surface flow helps to mediate levels of dissolved oxygen and the potential effects of eutrophication via nutrient inputs can be counteracted (Lake 2003). However, the comparatively stagnant water present during droughts might become choked by algal growth, compounding eutrophic processes (Lake 2003) and potentially altering nutrient cycling patterns (Austin and Strauss 2011). As organismal density increases in drought conditions, the amplified strength of biotic interactions could have cascading consequences that facilitate or reduce algal growth (Magoulick 2014). Additionally, the respiratory needs of organisms confined to refuges might exceed the dissolved oxygen levels present in eutrophic systems. Blooms of harmful algal species might also be of concern during droughts as toxins become increasingly concentrated as water volume decreases. In systems with significant agricultural use, irrigationmediated water withdrawals can increase drought frequency and severity (Palmer et al. 2006). As agricultural introduction of nitrogen and phosphorous to ground and surface waters accounts for a significant amount of inland eutrophic systems (Correll 1998), it is increasingly likely that drought and nutrient stressors co-occur. Additionally, stream ecosystems with significant nutrient pollution are further susceptible to additional stressors including fine sediment deposition and variations in water temperature (Lange et al.2013), and nutrients might influence community resilience in systems that experience regular hydrological variation (Murdock et al 2011).

Despite a large body of established literature exploring the individual effects of drought (e.g., Lake 2003), and nutrient pollution (e.g., Woodward et al. 2012), the fine-scale effects of multiple stressors on stream communities remain underexplored (Jackson et al. 2018). Here, we performed a manipulative experiment that explored the effects of seasonal drought and nutrient pollution on stream ecosystems. We hypothesize that drought will negatively affect fish and crayfish species, and that drought will amplify the detrimental effects (e.g., decreased dissolved oxygen levels) of nutrient pollution on fish species. However, we also expect that concentration effects in drought systems will help to stimulate algal production, potentially causing bottom-up trophic cascades and influencing overall system primary production. We also expect drought to decrease aspects of stream ecosystem functioning including leaf decomposition and invertebrate densities, however these might be offset by positive effects of nutrient enrichment. Finally, we expect that drought will affect the shallow and deep portions of the habitat differentially. Because aquatic ecosystems often experience anthropogenic degradation that includes multiple stressors, exploration of the ecology of these systems represents a necessary advancement in our understanding of disturbance ecology.

Methods

Experimental design

To test the effects of seasonal drought and nutrient pollution on stream ecosystem structure and function, we performed a fully factorial mesocosm experiment at the University of Arkansas biological greenhouse in the summer of 2017. Response variables included growth and survival of fish and crayfish species, chlorophyll a concentration, periphyton ash-free dry mass (AFDM), autotrophic index, sediment levels, and macroinvertebrate density. We also looked at measures of ecosystem functioning: net primary production and leaf litter decomposition.

Drought treatments consisted of water withdrawals over 3 days at a rate of 0.08 m/day until water was 0.25 m above the bottom of the deep end of the tanks. In these treatments, the substrate surface in the shallow portion of the tank was completely above the water line. Nutrient treatments involved enriching tanks to 1.0 mg/L of N (via the addition of $NaNO_3$) and 0.1 mg/L of P (via the addition of Na_2PO_4) (Sensu Evans-White et al. 2009). We housed the mesocosms in a climate-controlled bay under natural light in a 4 × 7 grid. Each of the four treatments—drought, nutrient enrichment, both stressors, and a no stressor control—had 7 replicates. Treatments were interspersed among the grid with a randomized starting point for each row

Each mesocosm consisted of a 416 L oval polyethylene tank (1.26 m long × 0.84 m wide × 0.49 m deep) with a mixed substratum of gravel and pebbles. Substratum was placed along a slope ranging from 0.10 to 0.32 m from the bottom of the tank so that ~⅓ of the benthic habitat was level and shallow (riffle), ~⅓ was sloped, and ~⅓ was level and deep (pool). Tanks were filled with municipal water and circulated by canister aquarium filters (Fluval 205 and 206; Hagen, Quebec, Canada). On May 26th, three weeks prior to the experiment, a slurry of scrubbed periphyton and stream water taken from Dye creek, Arkansas (35.94189,-94.18368) was added to each tank to facilitate algal and bacterial growth. Invertebrates were allowed to colonize the tanks naturally. Previous experiments have shown that Chironomidae readily colonize the mesocosms within the experimental time-frame (Ludlam and Magoulick 2009, Magoulick 2014, Lynch and Magoulick 2016). Fiberglass mesh (1 mm by 1 mm) lids were placed over each of the tanks and secured with clips to prevent escape.

Focal species selected for the mesocosm experiments represent a cross-section of Ozark stream community fauna and occupy multiple ecological and trophic roles; longear sunfish (*Lepomis megalotis*), an insectivorous mesopredator, central stoneroller (*Campostoma anomalum*), a primarily algivorous minnow, and ringed crayfish (*Faxonius neglectus*), an omnivore. In Ozark streams, longear sunfish prefer pool habitats while central stonerollers primarily inhabit riffles and runs (Robison and Buchannan 2020). The ringed crayfish is a substantial driver of freshwater ecosystem structure and functioning as both producers and consumers of biomass (Whitledge and Rabeni 1997, Wagner and Taylor 2008). All species are distributed widely though the focal region and co-occur naturally in the Ozark Highlands (Robison and Buchannan 2020, Pflieger 1996). Central stonerollers and longear sunfish were collected via backpack electrofishing from Scull and Mud creek in northwest Arkansas, respectively (36.06303, 94.09446; 36.120277, -94.153912). Ringed crayfish were collected via kick seining from Tanyard Creek, Arkansas (36.475565, -94.254442). Each mesocosm contained 18 individuals; 3 sunfish, 10 stonerollers, and 5 crayfish. These ratios coincide with naturally observed densities (Ludlam and Magoulick 2009). Length (total length for fish (TL) and carapace length for crayfish (CL)) and mass of each individual was recorded, and initial mean size for each species in all mesocosms was calculated. Initial mean size was similar for all treatments (~4.5 ± 2.6 g for stonerollers, ~17.5 ± 15g for longear sunfish, ~5.5 ± 3.5g for ringed crayfish). Central stonerollers, longear sunfish, and ringed crayfish were added to the tanks on June 16th and allowed to acclimate for 5 days before water withdrawals for drought treatments began (on June 21st). Fish and crayfish were removed from the tanks on July 21st and mean length and mass were recorded.

Four 11 × 11 cm unglazed ceramic tiles were placed into each mesocosm for measurement of algal biomass and invertebrate colonization. Two tiles were placed into the permanently watered section of each mesocosm, and two were placed in the shallow end. Leaves were collected from a local sugar maple (*Acer saccharum*), air dried to constant weight, and assembled into four, 3-g bags (32 cm by 22 cm with ~2.5-mm mesh, Volm Companies, Antigo, Wisconsin) and two each were placed in the shallow (riffle) and deep (pool) habitats. Two, 7-cm long slits were cut into each bag to allow for crayfish access. Tiles and leaf packs were removed on July 21st. We calculated net primary production by taking dissolved oxygen and temperature readings using a YSI multiparameter sonde (YSI Incorporated, Yellow Springs, Ohio) every 2 hours for 24 hours starting at 6am on July 17th (Sensu Bolt 1996).

Laboratory methods

Periphyton scrubbed from the tiles at the conclusion of the experiment was diluted with a known quantity of water and mixed until homogeneous before a 10 mL subsample was removed and filtered onto pre-weighed glass fiber filters (Pall GF/F) and frozen until analysis. The remainder of the sample was searched for Chironomidae and density was calculated as individuals per cm^2. The filter was placed in 10 mL of 95% ethanol for extraction and spectrophotometric analysis of chlorophyll a concentration. The contents of the cuvette were evacuated back onto the filter and then dried for 24 hours at 100ºC to obtain dry mass before being combusted at 550ºC for 3 hours, rewetted, and dried to obtain sediment organic matter as ash-free dry mass (AFDM). Leafpacks were air dried and weighed to determine change in mass. Autotrophic index was calculated as the ratio of chlorophyll a to AFDM. Sediment levels were calculated as the mass of the filtered slurry after ashing.

Statistical analysis

Two-way analysis of variance (ANOVA) was used to assess the effects of drought and nutrient treatments on mean growth and survival of fish and crayfish, algal biomass, chironomid densities, sediment, and autotrophic index, net primary production, and leafpack decomposition. If there was no significant interaction between nutrient and drought treatments, one-way ANOVAs were used to examine main effects. We also performed multivariate analysis of variance (MANOVA) on fish and crayfish total growth (delta mass, delta length) and periphyton structure (chlorophyll a, AFDM, and autotrophic index) variables. Shallow and deep habitats were examined separately for periphyton response variables, leaf litter decomposition, and macroinvertebrate density. All statistical analyses were performed using SYSTAT version 13 (SYSTAT Software, San Jose, California) with an α of 0.05.

Results

Fish and crayfish growth and survival

Drought and nutrient pollution affected fish and crayfish differentially. For central stonerollers, we found no significant interaction for drought and nutrient treatments nor any significant main effects for delta length, delta mass, or survivorship variables (Figure 1, Table 1). For longear sunfish, we saw a significant positive multivariate effect of drought on growth, and a univariate, antagonistic interaction of growth and nutrient treatments on survivorship. No other longear sunfish variables were significantly affected by treatment (Figure 1, Table 1). For ringed crayfish, we observed a significant positive effect of nutrients on multivariate growth, but no additional interactive or main effects (Figure 1, Table 1).

Benthic community structure

In shallow habitats, drought had a negative effect on multivariate periphyton structure, as well as negative univariate effects on chlorophyll a concentration, sediment levels, chironomid density, and autotrophic index. We observed no interactive or nutrient main effects in shallow habitats (Figures 2, 3, Table 2). In deep habitats, drought had an overall positive effect on multivariate periphyton structure, as well as positive effects on chlorophyll a concentrations, ash free dry mass, and the autotrophic index (Figure 2, Table 2). Nutrients had a negative effect on ash free dry mass in deep habitats, but an overall positive influence on multivariate periphyton variables (Figure 2, Table 2). Drought and nutrient pollution interacted synergistically to positively influence multivariate periphyton structure. We observed no other significant interactive or main effect of stressors in deep habitats. (Figures 2, 3, Table 1).

Ecosystem functioning

Drought had a negative influence on leaf litter decomposition in shallow habitats. However, we observed no effect of nutrients, nor any interactive effect on leaf decomposition (Figure 3). We did not observe any effect of treatment on net primary production or leaf decay in deep habitats. (Figure 3)

Discussion

We found that drought, nutrients, and the combined effects of these stressors affected many aspects of stream ecosystem structure and functioning. Empirical documentation of stressor interaction in freshwater systems is less robust than marine systems, and most studies have found antagonistic interactions (Jackson et al. 2016). While the inherent environmental heterogeneity of lotic systems might foster a greater potential for evolutionary adaptations to multiple stressors (Jackson et al. 2016), our study found that stressor interactions were highly context dependent, and differentially impacted ecosystem structure and function based largely on trophic position. Though many examinations of multiple stressor systems focus on population-level responses (Omerod et al. 2010), community and ecosystem-scale examinations can elucidate the impact of individual and multiple stressors, even if individual population responses are obscured (Van den Brink et al. 2016, Burdon et al. 2016).

Our study found that drought negatively influenced many portions of the benthic community in shallow habitats. As in real systems exposed to drying, our tiles and leaf packs were above the waterline for portions of the experiment, and these results coincide with previous examinations of drought systems. Previous field (e.g., Thomas et al. 2001, Timoner et al. 2014,Klamt et al. 2020) and mesocosm (Magoulick 2014, Lynch and Magoulick 2016) studies have shown that drought can negatively affect algal communities (Datry et al. 2011). Additionally, drought can negatively impact macroinvertebrate taxa (Boulton 2003, Finn et al. 2009), cause a decrease in the autotrophic index as photosynthetic components of the periphyton die (Magoulick 2014), and slow the decomposition of leaf litter (Datry et al. 2011, Magoulick 2014). While previous research has connected drought to increased levels of sedimentation (e.g., Rolls et al. 2012), drought decreased sediment levels in our study. However, closed-system mesocosm experiments that examine drought might not allow sufficient time for sediment accumulation prior to water withdrawals (Lynch and Magoulick 2016).

Surprisingly, drought treatments positively affected chlorophyll a concentrations, ash free dry mass, and the autotrophic index in deep habitats. Many algal species often persist in pool refuges during drought, and pool habitats can provide important source populations for algal recolonization after drought events (Robson 2000). As our drought treatments included wetted pools, they might have served as refuges for algal species in our experiment and facilitated their population growth. Drought decreased—though not significantly—chironomid densities (p=.052) in deep habitats. Concentration effects likely increased the predatory influences of longear sunfish and ringed crayfish on chironomids, causing a top-down cascade that released algal communities from grazing pressures (Magoulick 2014, Passy and Larson 2019). Additionally, increased light penetration into the deep portions of the tank during drought treatments might have positively increased periphyton variables (Gordon and McCluney 1975). Furthermore, concentration effects and increased grazing pressures in drought treatments might have differentially influenced algal community composition. Previous work has demonstrated that grazing pressures can influence algal community structure (Power et al. 1988) and grazing during droughts can further alter periphyton composition (Thomas et al. 2001, Kohler et al 2011). Increased grazing by fish species might also reduce the amount of senescent algal cells, increasing chlorophyll a concentrations (Jacoby 1997, Taylor et al. 2012, Passy and Larson 2019). A decrease in senescent cells via grazing coupled with increased sunlight penetration and a suppression of chironomids might explain the positive effect of drought on periphyton in our study. Drought also impacted some aspects of ecosystem functioning in our experiment. Previous work has shown that drought can negatively impact leaf breakdown (Datry et al. 2011, Magoulick 2014), and our drought treatments produced similar patterns. Net primary production was unaffected by drought treatment. Similar mesocosm experiments have shown drought negatively impacts NPP (Magoulick 2014). However, our experimental design necessitated that the pump output provide aeration to prevent fish mortality. Accordingly, the increase in dissolved oxygen might have masked treatment effects.

Fish and crayfish were largely drought tolerant in our study. Our focal species are native to the Ozark region of northwestern Arkansas (Robison and Buchannan 2020). Streams in this region are prone to seasonal drying and desiccation (Magoulick and Kobza 2003) and it is likely that many fish and crayfish in this region have evolved adaptations to drought events (Hodges and Magoulick 2011). Surprisingly, longear sunfish growth was positively affected by drought conditions in our study. Because drought positively affected many aspects of the benthic community, we suspect longear sunfish growth was supplemented by increased resource availability. This result contrasts previous work that showed that drought can have a negative impact on fish and crayfish body size (Taylor 1983, Walters and Post 2002, Lynch and Magoulick 2016). Furthermore, previous studies (e.g. Allen 1974, Ramalho et al. 2008) have demonstrated that density-dependent factors can negatively affect growth and survivorship of fish and crayfish. Because drought treatments increased relative density, we anticipated density-dependent responses (Lynch and Magoulick 2016). However, bottom-up increases in resources in drought tanks might have been sufficient to ameliorate any density-dependent effects. However, as we only looked at the changes in mean length and mass through the experiment, some treatment effects might be masked by size-based mortality.

Nutrient treatments caused the largest net increase in mass for all species, however, only ringed crayfish showed statistically significant differences in growth resulting from nutrient additions. Bottom-up trophic cascades are well documented in the literature (e.g., Power 1992), and nutrient additions can cause an overall increase in resource availability if the system is nutrient-limited (Schindler 1977). In our study, nutrient addition increased multivariate periphyton structure in deep habitats. Though we did not see a direct influence of nutrients on chironomids, the positive effect of nutrients on crayfish growth—and the subsequent increase in grazing on both algae and chironomids that led to a decrease of ash free dry mass—suggests cascading trophic interactions. Previous work has demonstrated that an increase in biomass at higher trophic levels can affect the algal resources even in nutrient enriched systems (Hughes et al. 2013). As crayfish both directly consume algal stocks, and feed on chironomid grazers (Momot 1995), they can impact food web structure across multiple trophic levels—which could explain their nutrient response. Central stonerollers showed no nutrient response in our treatments. While both central stonerollers (Gelwick and Matthews 1997) and ringed crayfish (Magoulick 2014) can influence algal communities, crayfish are a key driver of ecosystem processes in stream systems (Momot 1995) and can process larger quantities of algal and detrital biomass than stonerollers (Evans-White et al. 2001).

Drought and nutrient treatments interacted antagonistically on longear sunfish survival. Nutrients caused a non-significant net increase in longear sunfish biomass (p=.059), which likely increased competition for food resources as energetic requirements increased, thus negatively influencing survival rates. However, the increased resource availability of drought treatments ameliorated competitive interactions and increased survival. Drought and nutrient treatments interacted synergistically in shaping multivariate periphyton structure—causing an overall increase in photosynthetic portions of the periphyton. The suppression of chironomids by increased predation pressures during drought coupled with the net increase in photosynthetic algae resulting from nutrient additions synergistically increased basal resources. While these effects positively influenced fish and crayfish species in our study, previous work has shown that drought and nutrient pollution might interact synergistically to negatively influence population dynamics (Lake 2003). However, negative effects of nutrient enrichment tend to be more influential over longer time-scales than our experiment examined (Donohue et al. 2009, Romero et al 2019). Our results reinforce the findings of other studies (e.g., Chase 2007, Donohue et al. 2009) that demonstrate drought and nutrient pollution can influence ecosystem structure and function in aquatic systems. While the drought-mediated increases in periphyton variables helped to ameliorate some negative effects of nutrient enrichment on fish and crayfish populations, the additive relationship between drought and nutrient pollution on periphyton variables might have long term impacts on population and community dynamics. Furthermore, increased drought severity, increased nutrient levels, or longer observational scales would likely elicit different effects than the ones our experiment produced. Accordingly, additional examination of how these stressors interact in a variety of systems is warranted.

Our work highlights the complexity of drought and nutrient effects on stream communities and emphasizes that our understanding of individual stressors might not adequately inform our knowledge of multi-stressor systems. As individual stressors can differentially interact on varying aspects of the food web simultaneously, management or conservation strategies that incorporate only one stressor might be inadequate to conserve stream systems. Because anthropogenic development and resource use is likely to increase the relative effects of drought and nutrient pollution on stream systems, additional experimental, observational, and modelling work is necessary to clarify the mechanisms of compounded stressors.

Acknowledgements

Partial funding for this experiment was provided by the Arkansas Game and Fish Commission and United States Geological Survey. We thank Chris Middaugh, Leah Bayer, Nathan Quimbo, Jessica Clark, Katherine Wynne, and Allyn Dodd for their field and laboratory help. We also thank Michelle Evans-White for her comments on this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of the University of Arkansas Animal Care and Use Committee protocol #16055.

Conflict of interest

There are no conflicts of interest.

Data availability

Data for this study will be stored at the University of Arkansas and available upon request.

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Appendices

Tables and Figures

Table 1: Probability values associated with multivariate analysis of variance (MANOVA) for the effect of drought and nutrient enrichment on overall change of growth (change in mass and length) and analysis of variance (ANOVA) for the effect of drought and nutrient enrichment on change in length, change in mass, and survival of Central Stoneroller (CSR), Longear Sunfish (LES), and Ringed Crayfish (NEG). Bold highlights significant values ($p < 0.05$ for ANOVAs; Pillai's Trace test used for MANOVAs).

Variable and Species	**Overall effect (growth)**	**ΔMass**	**ΔLength**	**Survivorship**
CSR				
Drought	0.240	0.192	0.224	0.217
Nutrients	0.144	0.410	0.074	0.909
Drought x Nutrients	0.532	0.257	0.879	0.909
LES				
Drought	**0.035**	0.484	0.157	0.999
Nutrients	0.109	0.059	0.535	0.111
Drought x Nutrients	0.839	0.552	0.641	**0.049**
NEG				
Drought	0.580	0.521	0.958	0.635
Nutrients	**0.035**	0.077	0.985	0.635
Drought x Nutrients	0.187	0.293	0.075	0.874

Table 2: Probability values associated with multivariate analysis of variance (MANOVA) and analyses of variance (ANOVA) for effects of drought and nutrient enrichment on periphyton variables (chlorophyll a[Chl a],ash-free dry mass [AFDM], autotrophic index [AI]). Bold highlights significant values ($p < 0.05$ for ANOVAs; Pillai's Trace test used MANOVAs).

Variable and Habitat	**Overall effect (periphyton)**	**Chl a**	**AFDM**	**Chironimids**	**AI**	**Sediment**	**Leaves**
Shallow Habitats							
Drought	**<.001**	**<.001**	0.863	**0.007**	**<.001**	**0.031**	**<.001**
Nutrients	0.343	0.974	0.366	0.545	0.679	0.483	0.999
Drought x Nutrients	0.485	0.114	0.615	0.795	0.178	0.542	0.132
Deep Habitats							
Drought	**<.001**	**<.001**	**0.004**	0.052	**<.001**	0.766	0.167
Nutrients	**0.041**	0.180	**0.017**	0.765	0.364	0.332	0.243
Drought x Nutrients	**0.016**	0.378	0.060	0.533	0.169	0.757	0.742

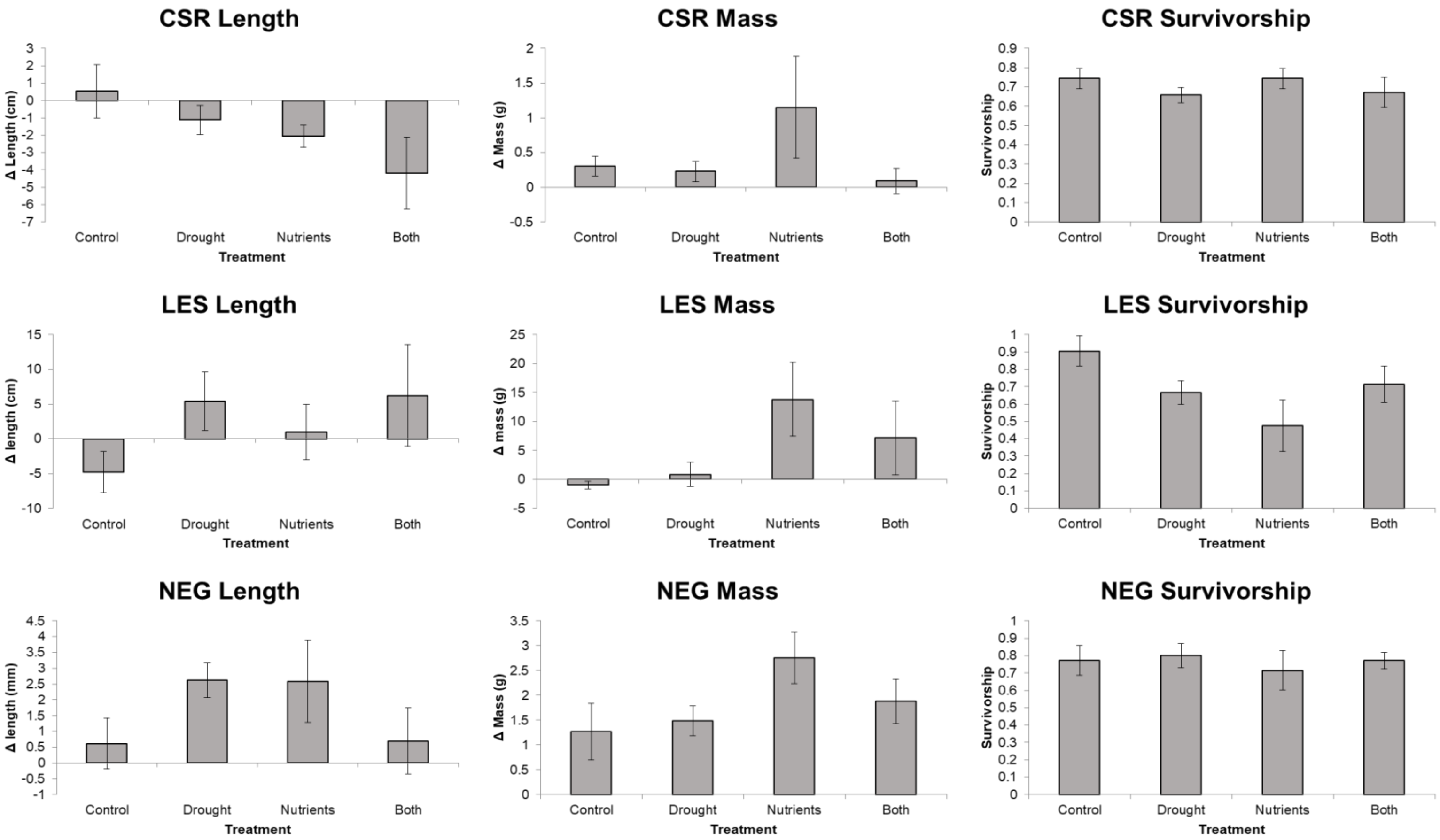

Figure 1: Change in length (left), mass (middle column), and survivorship (right) for Central Stonerollers (top), Longear Sunfish (middle row) and Ringed Crayfish (NEG, bottom). Error bars are standard error

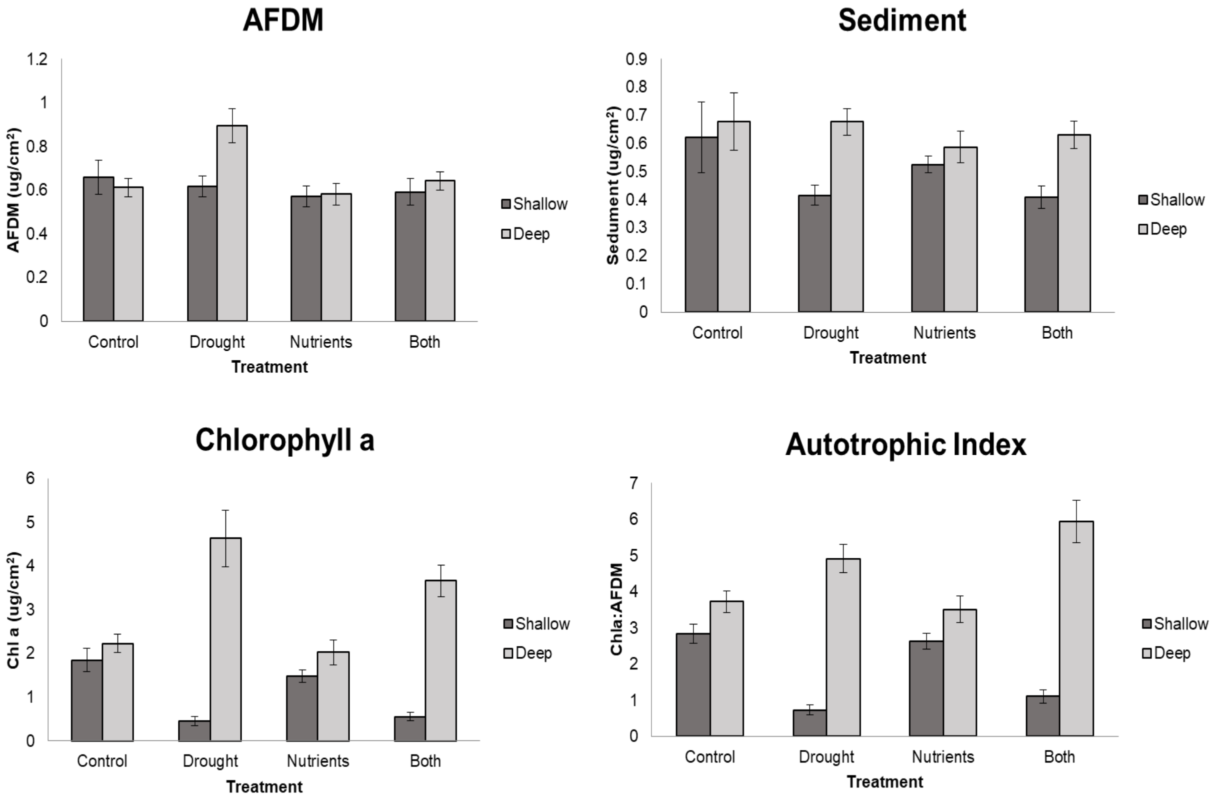

Figure 2: Ash free dry mass (AFDM, top left), Sediment levels (top right), Chlorophyll a (Chl a,bottom left), and Autotrophic Index (bottom right) for shallow and deep habitats. Error bars represent standard error.

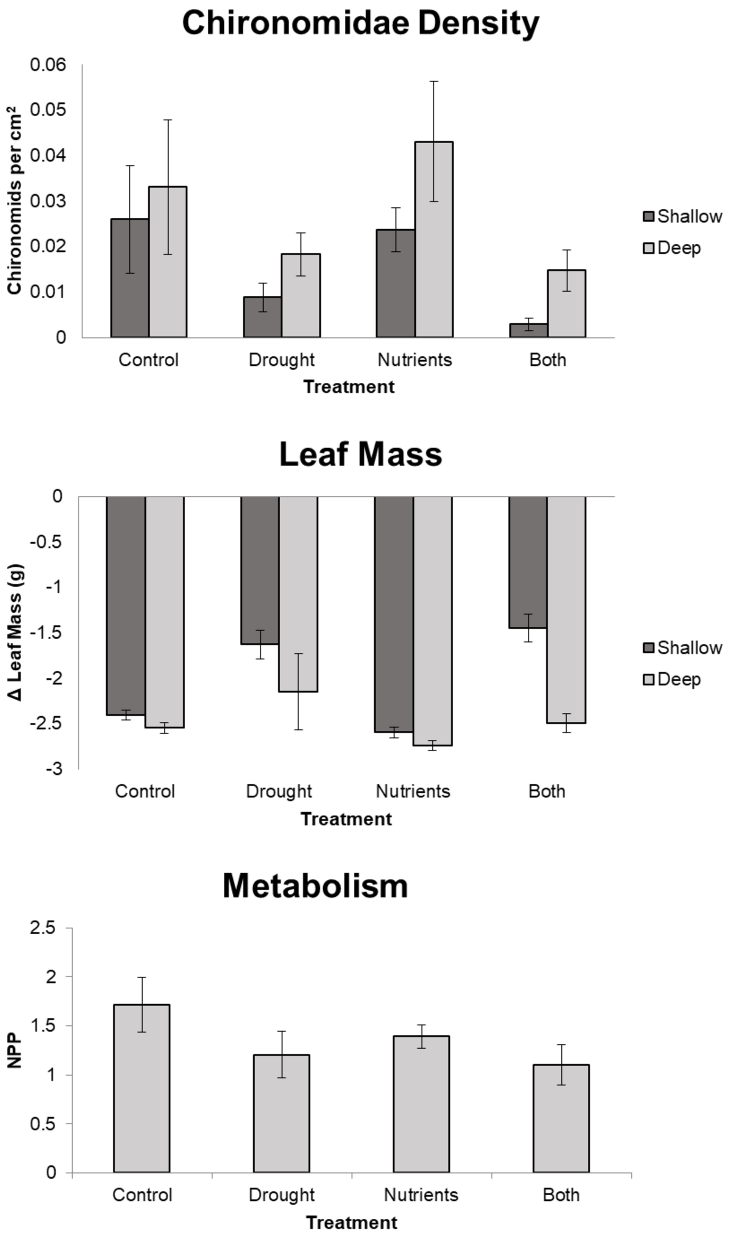

Figure 3: Chironomid density (top) and change in leaf mass (middle) for shallow and deep habitats; net primary production (bottom). Error bars represent standard error.

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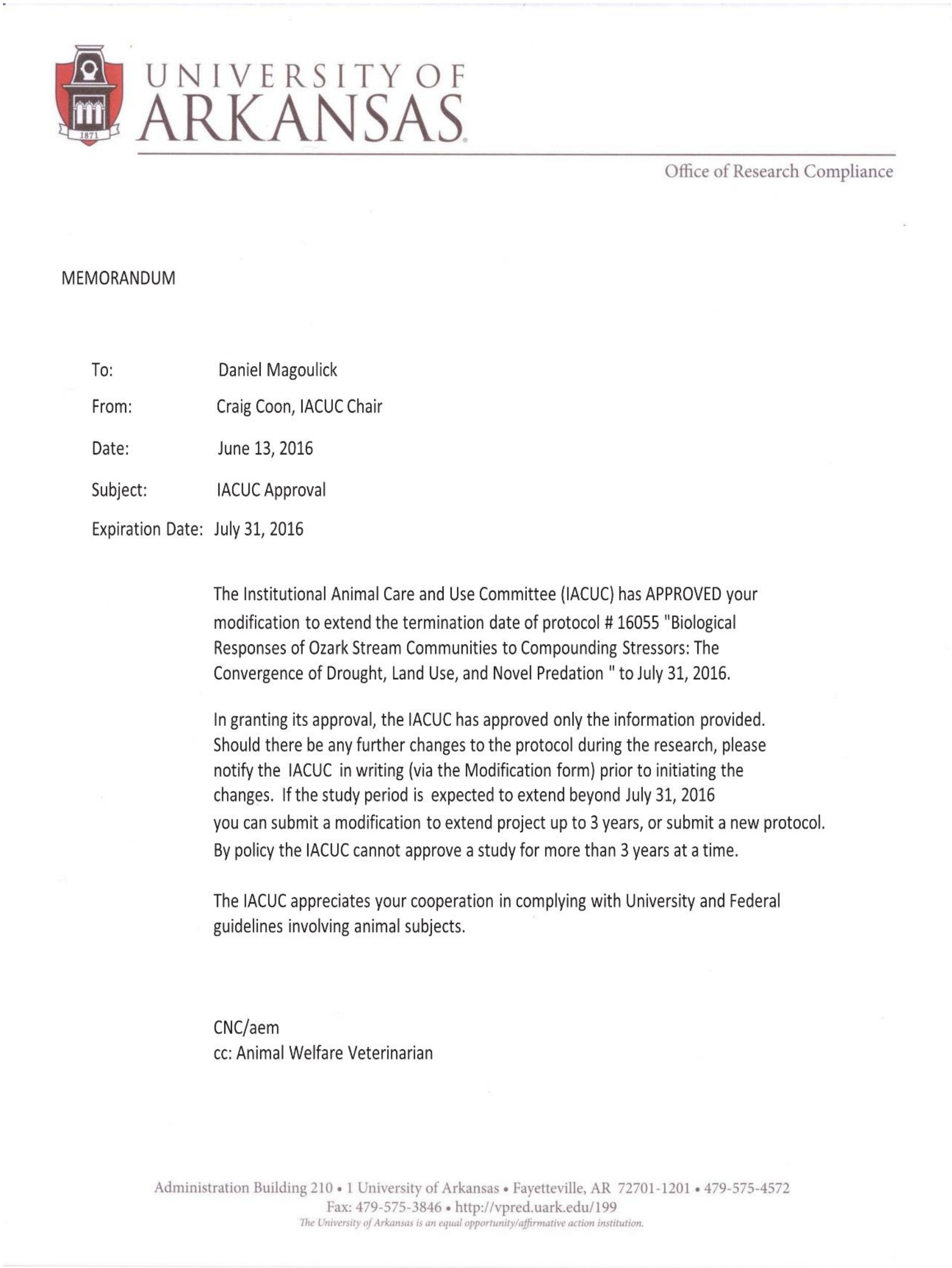

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ARKANSAS

Office of Research Compliance

MEMORANDUM

To: Daniel Magoulick

From: Craig Coon, IACUC Chair

Date: June 13, 2016

Subject: IACUC Approval

Expiration Date: July 31, 2016

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your modification to extend the termination date of protocol # 16055 "Biological Responses of Ozark Stream Communities to Compounding Stressors: The Convergence of Drought, Land Use, and Novel Predation " to July 31, 2016.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond July 31, 2016 you can submit a modification to extend project up to 3 years, or submit a new protocol. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem
cc: Animal Welfare Veterinarian

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Chapter 2: Effects of multiple disturbances on stream ecosystem structure and function: drought and predation

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Abstract

Drought and apex predation have diverse effects on stream community structure and function. While research has examined how these stressors shape stream communities individually, we know relatively little about if, and how, these stressors interact to influence stream systems. We performed a mesocosm experiment that explores the compounded effects of drought and increased apex predation on a subset of Ozark stream community fauna. While our study showed significant effects of individual stressors across a wide variety of response variables—including algal biomass, leaf litter decomposition, and macroinvertebrate density—drought and predation treatments did not produce significant statistical interaction on any measured variable. Our work demonstrates that individual stressors can impact stream community structure and function; however, stressor interactions are complex, and more work remains necessary to fully elucidate potential interactive effects.

Introduction

Two of the most common environmental and ecological disturbances to stream systems—drought, and invasive species—have significant and diverse impacts on communities and are often some of the most pervasive threats to fauna in these systems. While a broad foundation of research explores how these disturbances shape stream communities individually (e.g., Magoulick and Kobza 2003, Marcogliese et al. 2009, Albins and Hixon 2013), little research has examined how these disturbances might interact (Omerod et al. 2010, Jackson et al. 2016). As it is increasingly likely that freshwater systems experience multifaceted anthropogenic degradation, a better understanding of the ecology of streams that experience multiple, concurrent disturbances is necessary to stem biodiversity loss and protect water resources.

Drought affects aquatic ecosystems on every continent and imposes a diverse array of environmental and ecological effects that can influence population and community dynamics (Townsend and Hildrew 1994, Beche et al. 2009). In addition to mortality brought on by a direct loss of habitat due to decreased water volume, aquatic ecosystems undergo several physical, chemical, and hydrological changes during drought—many of which illicit direct biological responses (Lake 2003). For instance, droughts can alter important spatially-mediated community characteristics (i.e., those dependent on water depth) and increase population densities via concentration effects (Magoulick 2000, Magoulick and Kobza 2003). Under these conditions, the relative strength of biotic interactions could increase dramatically (Magoulick and Kobza 2003).

To persist through drought events, organisms must make use of refuge habitats (Magoulick and Kobza 2003). The riffle-pool morphology of many forested streams might be an important factor in how aquatic species evolved to deal with hydrological disturbance (Davey and Kelly 2007; Dekar and Magoulick 2007). Due to their increased volumes, pools may not fully dry during normal seasonal drought and provide important temporary habitats for many of the stream fauna (Matthews 1998). Accordingly, species that are normally obligate riffle- or run-dwellers may seek refuge in pools as streams dry. When confined to refugia, species are more prone to predation and might be more susceptible to additional disturbance factors (Magoulick and Kobza 2003). Additionally, drought has been shown to negatively affect algal populations (Timoner et al. 2014), and slow ecosystem processes such as leaf litter decomposition (Datry et al. 2011). While drying constitutes a significant stressor to stream populations, many species in systems prone to drought have evolved adaptations to survive harsh conditions experienced during drought and drying (Magoulick and Kobza 2003, Lake 2003, Hodges and Magoulick 2011).

Apex predators often play a keystone role within their ecosystem (Paine 1966; Paine 1974; Power et al. 1996). In freshwater streams, apex predation has been shown to illicit strong top-down trophic effects on grazers and primary production (Power et al. 1983; Power et al. 1988). Furthermore, as grazers can selectively affect competitive outcomes in algal species leading to shifts in community composition (Power and Matthews. 1983; Matthews et al. 1987), mediate nutrient cycling (Urabe 1993), and facilitate the longitudinal transfer of organic materials (Vannote et al. 1980), the suppression of grazers by predators can dramatically influence community structure and function. While all predators exert some top down ecological effects on their trophic system, the degree by which freshwater predators stabilize or destabilize the food web is dependent on the magnitude of predation pressures coupled with the ability of prey species to avoid predation (Creed 2006).

Invasive species have significant and often detrimental effects across ecosystems (Clavero and Garcia-Berthou 2005). Invasive predators may exert predation pressures that exceed naturally sustainable levels (Doherty et al. 2016). Furthermore, when prey are sufficiently naïve to an invasive predator, they may fail to adapt appropriate defensive mechanisms to avoid predation (Freeman and Byers 2006). Conversely, when an invasive predator is recognized, prey species might fail to appropriately abandon unnecessary defensive measures—often resulting in decreased biological fitness.

Smallmouth bass (*Micropterus dolomieu*) are apex predators in many low order, streams within the Ozark Highlands of Arkansas, Missouri, and Oklahoma, USA (Robinson and Buchannan 2020). However, introduction of other bass species including the largemouth bass (*Micropterus salmoides*) represent a significant and often overlooked ecological threat (Stein and Magnuson 1976; Harvey et al. 1988). Largemouth bass are often stocked as sport fish for anglers (Maceina et al. 1988). Accordingly, their potential invasion impacts are largely ignored by managers when compared to invasive species from other continents (Jackson 2002). Because largemouth and smallmouth bass have different energetic and nutritional requirements (Anderson et al. 1984), and prey species have been shown to have differential behavioral responses to the presence of either predator (Harvey et al. 1998), the potential invasion impacts of largemouth bass into systems traditionally inhabited solely by smallmouth bass could have important effects on stream communities.

As surviving individuals migrate into remaining waters during drought events, overall biotic density increases (Matthews 1998); causing the frequency and strength of biotic interactions such as predation and competition to increase accordingly (Matthews 1998). Under extreme disturbance levels, the outcome of biotic interactions might change to reflect individual adaptations to drought (Davey et al. 2006) and organisms might undergo significant behavioral changes—including the loss of defensive and social behaviors (Fischer and Ohl 2005). Furthermore, the unavailability of refuge habitat has been shown to destabilize systems with high predation pressures (Creed 2006). Because drought events decrease habitat availability on the micro and mesohabitat scale, and predation is a significant driver of habitat selection

(Magoulick 2004), it is reasonable to assume that increased predation pressures imposed by a novel apex predator might be magnified under drought conditions. Furthermore, an excessive suppression of primary consumers in post-disturbance systems by increased predation might further alter system return trajectories (Murdock et al. 2010). Additionally, unnatural disturbance regimes might facilitate additional biological invasions (Scoppetone et al. 2005).

Despite the multitude of studies exploring the individual ecological dynamics of drought (Magoulick and Kobza 2003), and apex predation (Marcogliese et al. 2009, Salo et al. 2007, Albins and Hixon 2013), relatively little is known about the interplay of these disturbances on freshwater fish communities (Omerod et a. 2010). Here, we perform a manipulative experiment to examine the concurrent effects of drought and novel predation on several aspects of stream community structure and function. We hypothesize that drought will negatively affect the growth and survivorship of fish and crayfish, as well as negatively impact the benthic community. We also hypothesize that largemouth bass will exert more predatory pressure than their native counterpart, the small mouth bass—with cascading trophic implications. Finally, we predict that drought treatments might further amplify the strength of their predation. Concurrent disturbances might interact synergistically or antagonistically (Paine 1998, Jackson et al. 2016), therefore studies of individual disturbances might not sufficiently inform our knowledge of severely degraded systems (Christiansen et al. 2006). Because global aquatic ecosystems—especially in developed countries—often experience multifaceted anthropogenic degradation, an exploration of the ecology of these systems represents an increasingly necessary area of expansion to our understanding of disturbances.

Methods

Experimental design

To test the effects of drought (control or drought) and increased predatory pressures (smallmouth bass or largemouth bass presence) on stream ecosystem structure and function, we performed a fully factorial mesocosm experiment at the University of Arkansas biological greenhouse in the summer of 2016. Each of the four treatments had seven replicates; however, one tank in the smallmouth drought treatment was excluded because of bass mortality. Response variables included growth and survival of fish and crayfish species, leaf decomposition, chlorophyll a concentration, periphyton ash-free dry mass (AFDM), autotrophic index, sediment levels, leaf litter decomposition, and macroinvertebrate density.

We housed the mesocosms in a climate-controlled bay under natural light in a 4 × 7 grid. Each mesocosm consisted of a 416 L oval polyethylene tank (1.26 m long × 0.84 m wide × 0.49 m deep) with a mixed substratum of gravel and pebbles. Substratum was placed along a slope ranging from 0.10 to 0.32 m from the bottom of the tank so that ~⅓ of the benthic habitat was level and shallow (riffle), ⅓ was sloped, and ⅓ was level and deep (pool). Water was circulated by canister aquarium filters (Fluval 205 and 206; Hagen, Quebec, Canada). Three weeks prior to the experiment, on June 5th, a slurry of scrubbed periphyton and stream water taken from Dye creek, Arkansas (35.94189,-94.18368) was added to each tank to facilitate algal and bacterial growth. Invertebrates were allowed to colonize the tanks naturally. Previous experiments have shown that Chironomidae readily colonize the mesocosms within the experimental time-frame (Ludlam and Magoulick 2010, Magoulick 2014, Lynch and Magoulick 2015). Fiberglass mesh (1 mm by 1 mm) lids were placed over each of the tanks and secured with clips to prevent escape.

Drought treatments consisted of water withdrawals over 3 days at a rate of 0.083 m/day until water was 0.15 m above the bottom of the deep end of the tanks. In these treatments, the shallow portion of the tank was completely above the water line. Apex predation treatments consisted of the addition of one predator (smallmouth bass or largemouth bass) per mesocosm.

Treatments were interspersed among the 4 x 7 grid with a randomized starting point for each row.

Focal species selected for the mesocosm experiments represent a cross-section of Ozark stream community fauna and occupy multiple ecological and trophic roles; longear sunfish (*Lepomis megalotis*), central stoneroller (*Campostoma anomalum*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*) and ringed crayfish (*Faxonius neglectus*). All prey species co-occur naturally in the Ozark Highlands (Robinson and Buchannan 1988). Central stonerollers and longear sunfish were collected via backpack electrofishing from Scull and Mud creek in northwest Arkansas respectively (36.06303, 94.09446; 36.120277, -94.153912). Smallmouth bass were collected via angling from Big Sugar creek in southern Missouri (36.596817, -94.374668). Largemouth bass were collected via boat electrofishing in Lake Rayburn, Arkansas (36.462942, -94.240060). Ringed crayfish were collected via kick seining from Tanyard Creek, Arkansas (36.475565, -94.254442). Each mesocosm contained 19 individuals; 1 bass, 3 sunfish, 10 stonerollers, and 5 crayfish. These ratios coincide with naturally observed densities (Ludlam and Magoulick 2009). Length and mass of each individual was recorded, and initial mean size for each species in all mesocosms was calculated. Fish species lengths were recorded as total length while crayfish were recorded as carapace length. Initial mean size was similar for all treatments (~8 ± 1.58 g for central stonerollers, ~25 ± 13.70 g for longear sunfish, ~9 ± 2.78 g for ringed crayfish). Central stonerollers, longear sunfish and ringed crayfish were added to the tanks on June 26th and allowed to acclimate for 5 days before bass were added. Drought treatments began 5 days later (July 6th). Fish and crayfish were removed from the tanks on July 24th and mean length and mass were recorded.

Four 11 × 11 cm unglazed ceramic tiles were placed into each mesocosm for measurement of algal biomass and invertebrate colonization. Two tiles were placed into the permanently watered section of each mesocosm, and two were placed in the shallow end. Leaves were collected from a local sugar maple (*Acer saccharum*), air dried to constant weight, and assembled into 3 g bags (32 cm by 22 cm with ~2.5 mm mesh, Volm Companies, Antigo, Wisconsin). Two 7 cm long slits were cut into each bag to allow for crayfish access. Four leaf packs were placed into each mesocosm for measurement of leaf decomposition—two each in the riffle and pool habitats. Tiles and leaf packs were removed on July 24th.

Laboratory methods

Periphyton scrubbed from the tiles at the conclusion of the experiment was diluted with a known quantity of water and mixed until homogeneous before a 10 mL subsample was removed and filtered onto pre-weighed glass fiber filters (Pall GF/F). The remainder of the sample was searched for Chironomidae and density was calculated as individuals per cm^2. The filter was placed in 10 mL of 95% ethanol for extraction and spectrophotometric analysis of chlorophyll a concentration. The contents of the cuvette were evacuated back onto the filter and then dried for 24 hours at 100ºC to obtain dry mass before being combusted at 550ºC for 3 hours, rewetted, and dried to obtain sediment organic matter as ash-free dry mass (AFDM). Leafpacks were air dried and weighed to determine change in mass. Autotrophic index was calculated as the ratio of chlorophyll a to AFDM. Sediment levels were calculated as the mass of the filtered slurry after ashing.

Statistical analysis

Two-way analysis of variance (ANOVA) was used to assess the effects of drought and predation treatments on mean growth and survival, algal biomass, leafpack decomposition, chironomid densities, sediment, and autotrophic index. If there was no significant interaction between predator and drought treatments, one-way ANOVAS were used to examine main effects. We also performed multivariate analysis of variance (MANOVA) on fish and crayfish total growth (delta mass, delta length) and periphyton structure (chlorophyll a, AFDM, and autotrophic index) variables. Shallow and deep habitats were examined separately for periphyton response variables, leaf litter, and macroinvertebrate colonization. All statistical analysis was performed using SYSTAT version 13 (SYSTAT Software, San Jose, California) with an α of .05.

Results

Fish and crayfish growth and survival

We found no significant univariate or multivariate interaction for drought and predation treatments or significant univariate or multivariate main effects for delta length and delta mass of all fish and crayfish species ($p>.05$) (Figures1,2,3). Likewise, survival of prey species was not significantly different across treatments (Figures 1,2,3) ($p>.05$). However, in both predation treatments, central stoneroller survivorship was very low and, in many cases, suffered complete predatory mortality by the end of the experiment. Conversely, crayfish survivorship, while similar across treatments, was significantly higher than central stoneroller survivorship (Figure 6) indicating differential predation. Across all treatments, both bass species lost weight, but drought did not influence bass growth (Figures 6).

Periphyton, autotrophic index, chironomids, and leaf litter

In shallow habitats, we observed no significant univariate or multivariate interaction between drought and predation treatments ($p > .05$). However, largemouth-control treatments had significantly higher levels of chlorophyll a than largemouth-drought treatments, but not smallmouth-drought treatments; and smallmouth control-treatments were not significantly different to drought treatments (Figure 4) ($p < .001$). The autotrophic index was significantly affected by drought treatment, but not by bass species (Figure 4) ($p < .001$). Likewise, chironomid density was highest in the non-drought treatments, but did not significantly differ by bass species (Figure 5)($p < .001$). Leaf litter decomposition was lower in the drought treatments, but bass species had no effect on decomposition (Figure 5)($p = .053$). AFDM did not differ significantly by treatment (Figure 4), however largemouth control treatments had significantly higher sediment levels than smallmouth drought treatments (Figure 4) ($p=.006$). There was a negative effect of drought on multivariate periphyton structure variables in shallow habitats ($p = .001$), however predator species had no effect on periphyton structure ($p < .05$). In deep habitats, we found no significant effect for any comparison ($p < .05$).

Discussion

Fish and Crayfish

We saw no effect of drought treatments on fish and crayfish growth and survival. All of the species in the present study are native to the Ozark region of Arkansas and Missouri which is prone to seasonal drought and drying (Robison and Buchannan 1998). Accordingly, the natural history of these organisms may have facilitated some measure of drought resistance (Magoulick and Kobza 2003, Larson and Magoulick 2008). However, our results differ from several previous studies which showed that drought can have an impact on fish and crayfish body size (Taylor 1982, Walters and Post 2002, Lynch and Magoulick 2016). As streams dry, many fish and crayfish species move into wetted pool refuges to persist through the drying event (Magoulick and Kobza 2003). As our tanks were constructed to maintain a deeper (pool) habitat even in drying treatments, refuge-seeking behaviors might have increased drought resistance. However, as individuals move into refuges, their relative density increases. Previous studies of fish (e.g., Allen 1974) and crayfish (e.g., Ramalho et al 2008) have demonstrated that density-dependent factors can negatively affect growth and survival. As our tanks were stocked with densities mimicking natural conditions (Dekar and Magoulick 2007, Ludlam and Magoulick

2009, Hodges and Magoulick 2011), we hypothesized drought treatments—and the subsequent increase in density—would elicit density-dependent responses (Lynch and Magoulick 2016). However, the relatively short length of the experiment, and the addition of predators seem to have mitigated these effects when species were not completely eradicated.

Predator species appear to be functionally redundant in our experiment, and both species exerted sufficient predatory pressures to nearly eradicate central stonerollers from our experimental tanks. However, previous studies have demonstrated that smallmouth bass and largemouth bass have differential energy requirements, and that prey respond differentially to these bass species (Anderson et al. 1984, Harvey et al. 1988). Our experimental design might have represented an idealized condition for predators (e.g., few refuge habitats, close proximity, increased prey density in drought treatments). Accordingly, these factors might lessen potential predatory advantages that largemouth bass possess.

Both bass species had a greater effect on stoneroller survivorship than crayfish survivorship. However, fish prey items are often of secondary importance to bass in the wild (Fedoruk 1966, Rabeni 1992, Probst et al 1984). This shift in prey selection might relate to differential searching and handling time of prey species. Previous work has demonstrated that both smallmouth and largemouth bass will alter dietary preferences based on their ability to capture and consume prey items (Stein et al. 1977, Savino and Stein 1989). Our experimental design might have altered predatory interactions by increasing the foraging effort required for crayfish prey above that of stonerollers. Additionally, fish prey often necessitates less handling time than crayfish prey (Werner 1974). Accordingly, the apparent dietary shift of both bass species might result from our experimental design altering the tradeoff between searching and handling time. Therefore, future *in situ* studies of bass diet when confined to pool refuges during drought might be instructive.

We did not observe any interactions between drought and predation treatments on fish and crayfish growth or survival. We expected that largemouth bass would be more effective predators (Harvey et al. 1998), and that their predatory impacts would be amplified in drought settings as droughts have been shown to amplify biotic interactions including predation (Matthews 1998). However, our study failed to capture a significant increase in predatory effects for either bass species. It is likely that our experimental design was insufficient to capture any compounded effects imposed by concurrent disturbances on growth and survival. The length of our experiment was restricted by bass survivorship and, thus, shorter than similar studies that observed differential growth and survival effects (e.g., Lynch and Magoulick 2016). One potential axis of drought and predation interaction that our study did not account for is the speed of consumption of prey items. By the end of our experiment, nearly all stoneroller prey had been consumed. Because of their differential energy requirements, it is reasonable to assume that smallmouth and largemouth bass might have consumed stonerollers at different rates. As foraging time is an important aspect of predator efficiency, the speed of and magnitude of predatory interactions might influence population dynamics at broader spatial and temporal scales than our experiment explored—especially if magnified during droughts. Because it was infeasible to measure the rate of consumption in the present study, we are unable to ascertain if drought and predator treatments interacted in this regard.

Benthic community structure and function

Our study found that drought significantly influenced many aspects of benthic ecosystem structure and function in shallow habitats. Largemouth bass control tanks had significantly higher chlorophyll a levels than both largemouth bass drought tanks and smallmouth bass drought tanks. Previous studies have shown that drought negatively affects algal biomass both in field (e.g., Timoner et al. 2014) and mesocosm (Magoulick 2014) settings. However, drought did not affect algal biomass in deep habitats. While drought can induce concentration effects as grazers move into remaining waters (Matthews 1988), we did not observe concentration effects in any of our measured variables. Nevertheless, algal species often persist in pool refuges during drought and pools provide important source populations for algal recolonization after drought events (Robson 2000). As hypothesized, drought also decreased chironomid densities, leaf litter decomposition, and autotrophic index in shallow habitats. Previous research has demonstrated that drought has negative impacts across a wide variety of macroinvertebrate taxa (Boulton 2003), can slow the decomposition of leaf litter (Datry et al. 2011), and cause a decrease in autotrophic index as algae die and the heterotrophic components of the periphyton persist (Magoulick 2014). Interestingly, sediment levels decreased in the smallmouth bass drought treatments. Previous research has connected drought and lower flows to increased levels of sedimentation (Rolls et al. 2012). However, mesocosm studies that examine drought might not allow sufficient time for sediment accumulation before drying (Lynch and Magoulick 2016).

We observed no significant effects of predator species on any benthic community variables. The bass-stoneroller-periphyton trophic link has been well established in stream systems (Power et al. 1988). As largemouth bass have higher energetic requirements (Anderson et al. 1984), we hypothesized their increased predatory pressures would have greater effects on lower trophic levels. However, both bass species nearly eradicated stonerollers from our experiment and we could not observe significant differences in their top-down pressures on periphyton response variables. Furthermore, bass species did not seem to influence longear sunfish foraging capabilities as we saw no difference in chironomid densities for either predator. By the end of our experiment, bass had relatively recently begun to switch to crayfish prey after the stoneroller population was exhausted. While crayfish represent a higher proportion of bass diets in the wild (Probst et al. 1984), our experiment saw bass focus primarily on stoneroller prey. As crayfish are generally more omnivorous than stonerollers, and have a greater effect on leaf litter breakdown, it is possible we could have seen greater impacts on chironomid density or leaf litter decay if we provided the bass with only crayfish prey items.

While we did not observe significant statistical interactions between drought and predators, several benthic response variables were seemingly affected by both treatments. For chlorophyll a in riffle habitats, largemouth bass control treatments were higher than all drought treatments; however, smallmouth bass control treatments were not significantly different than drought treatments. This might indicate that stonerollers persisted for longer in smallmouth treatments and thus had a greater overall effect on chlorophyll in those tanks prior to the drought. Alternatively, stonerollers could have more readily recognized smallmouth bass as predators and spent more time foraging in the riffles away from the bass as a defensive behavior prior to the riffles drying. Additionally, largemouth bass control treatments had higher levels of sediment than smallmouth bass drought treatments. Algivorous fish tend to resuspend sediment into the water column while foraging (Persson and Svennson 2006). If smallmouth bass allowed stonerollers to persist longer, the stonerollers could have resuspended more sediment through grazing prior to water withdrawals in drought tanks. However, we did not record behavioral patterns or rate of consumption, so future experiments are necessary to determine if either of these factors played a significant role. Nevertheless, these findings indicate that bass species could have implications for post-drought return trajectories for periphyton communities.

Conclusion

Our study reinforced the finding that drought affects many aspects of stream benthic communities, however, we found that smallmouth- and largemouth bass are functionally redundant predators in this setting. Furthermore, our study did not observe meaningful interactions between increased predation and drought on stream ecosystem structure and function. Our experiment was relatively short, and these disturbances might operate on larger geographic and temporal scales than our study effectively captured. The interaction of multiple disturbances on ecosystem structure and function is highly context dependent and can work synergistically or antagonistically in freshwater systems (Jackson et al. 2016). Additional work is necessary to further elucidate the roles that compounded disturbances have on stream systems at both the community and ecosystem level.

Acknowledgements

Partial funding for this experiment was provided by the United States Geological Survey, Sigma Xi, and the University of Oklahoma Biological Research Station. We thank Nicole Graham, Chris Middaugh, Brittney Fuller, Auriel Fournier, Joe Moore, and Scott Koenigbauer for their field and laboratory help.

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Appendices

Figures

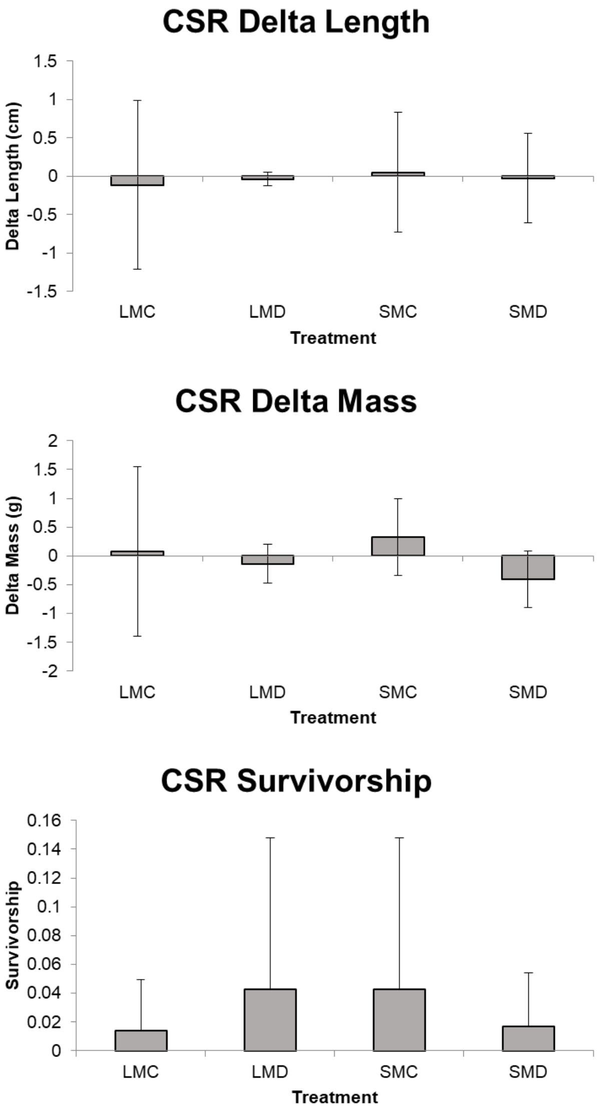
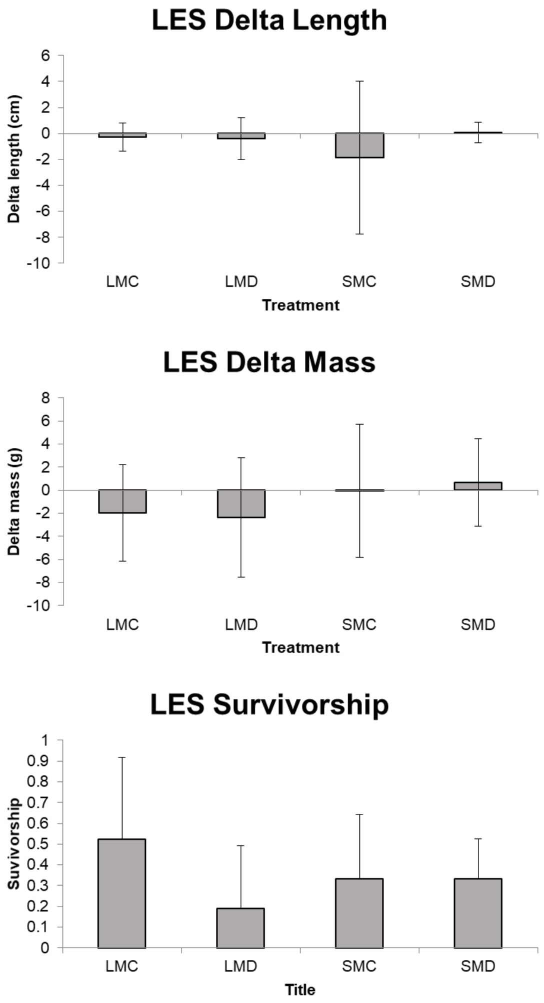


Figure 1: Change in length (top), mass (middle), and survivorship (bottom) for Central Stonerollers. LMC is Largemough Control, LMD is Largemouth Drought, SMC is Smallmouth control, SMD is smallmouth drought. Error bars are standard error.


LES Delta Length

LES Delta Mass

LES Survivorship

Figure 2: Change in length (top), mass (middle), and survivorship (bottom) for Longear Sunfish. Error bars are standard error.

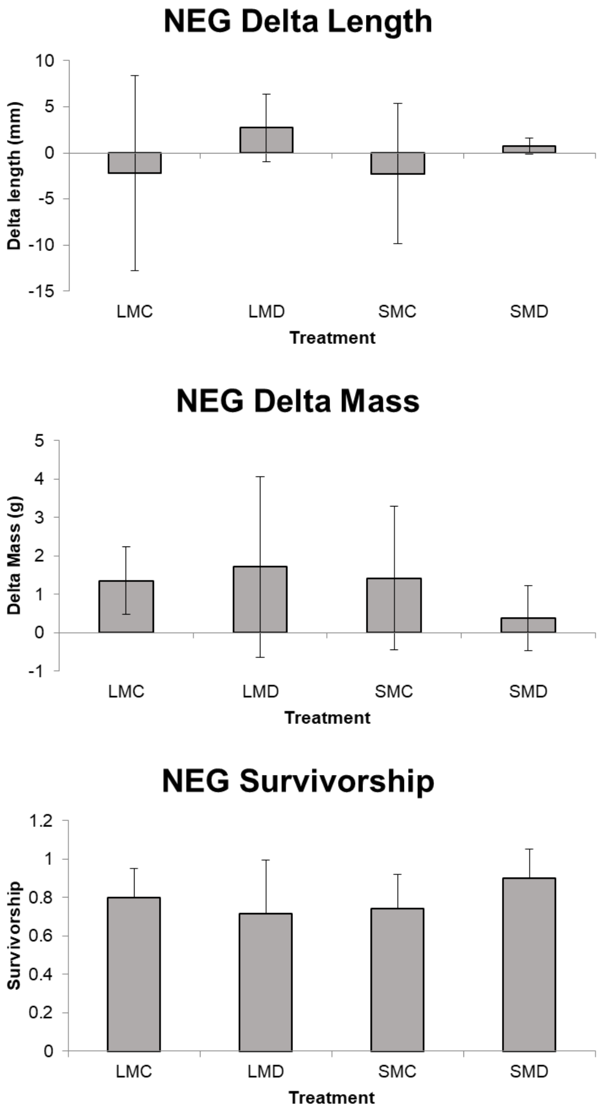


Figure 3: Change in length (top), mass (middle), and survivorship (bottom) for Ringed Crayfish. Error bars are standard error.

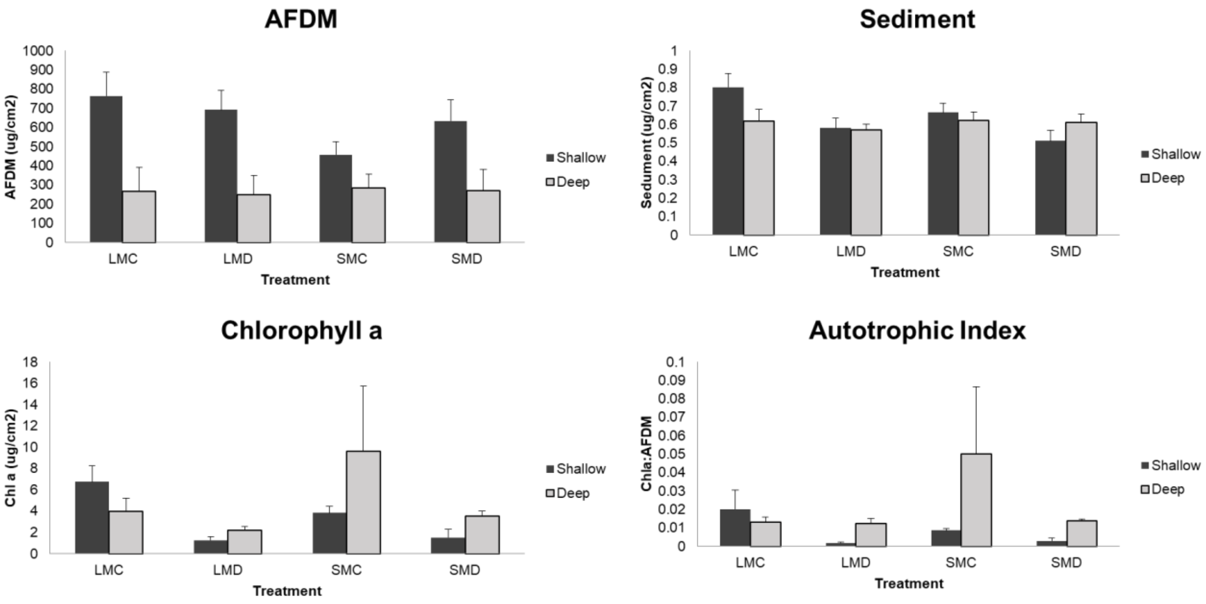


Figure 4: Ash free dry mass (AFDM, top left), Sediment levels (top right), Chlorophyll a (Bottom left), and Autotrophic Index (Bottom left) for shallow and deep habitats. Error bars represent standard error.

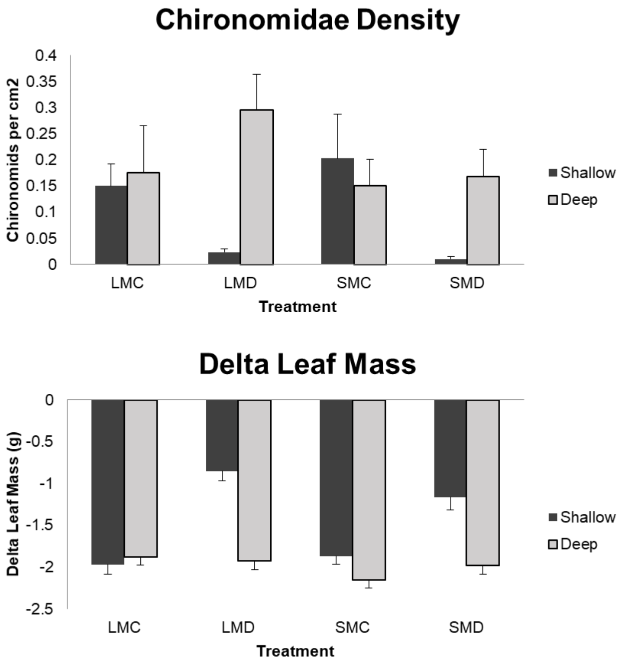


Figure 5: Chironomid density (top) and change in leaf mass (middle) for shallow and deep habitats. Error bars represent standard error.

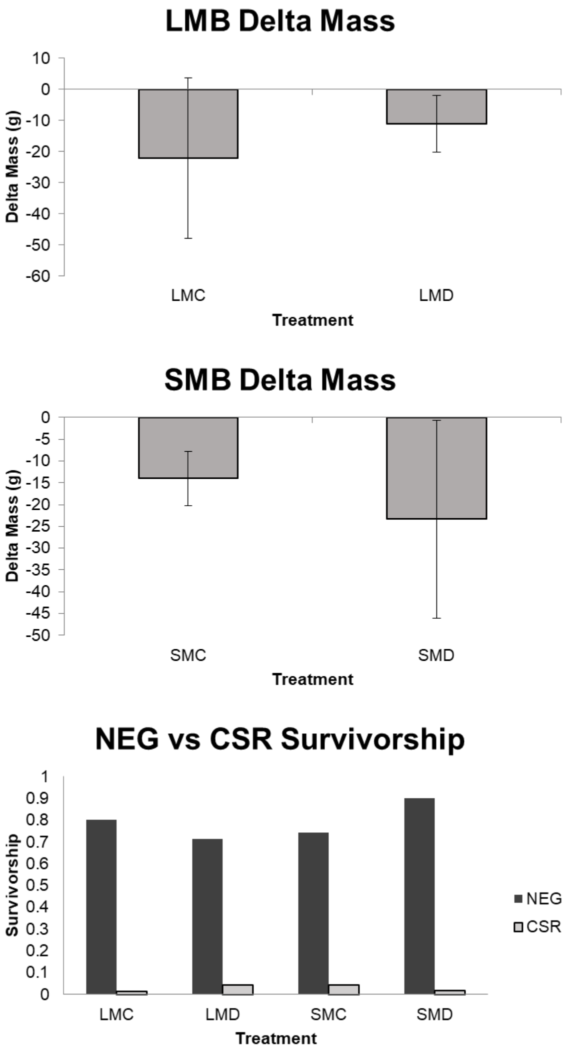
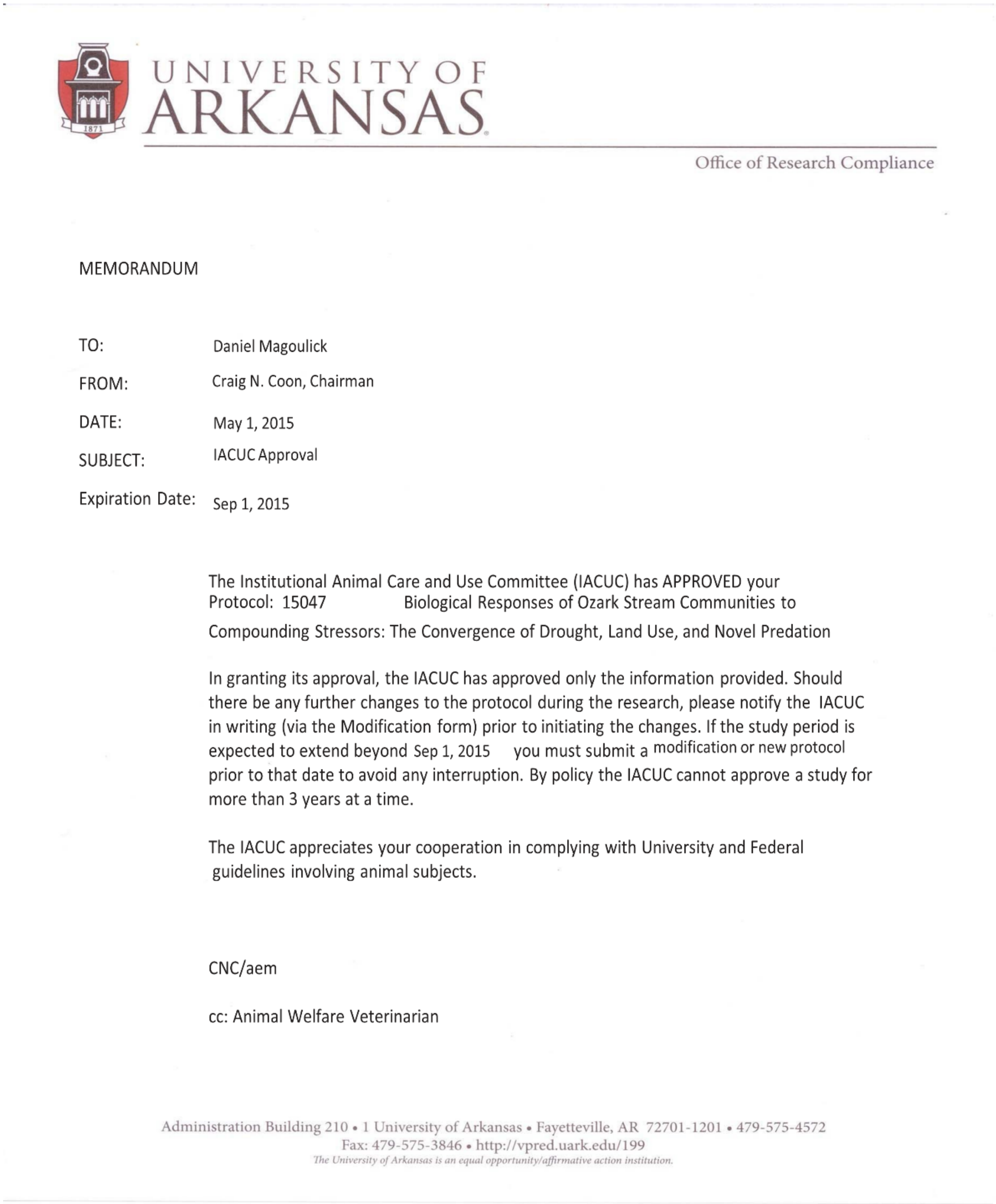


Figure 6: Survivorship for largemouth bass (top), smallmouth bass (middle) and differential prey survivorship between ringed crayfish and central stoneroller (bottom). Error bars represent standard error.

IACUC



UNIVERSITY OF ARKANSAS

Office of Research Compliance

MEMORANDUM

TO: Daniel Magoulick

FROM: Craig N. Coon, Chairman

DATE: May 1, 2015

SUBJECT: IACUC Approval

Expiration Date: Sep 1, 2015

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your Protocol: 15047 Biological Responses of Ozark Stream Communities to Compounding Stressors: The Convergence of Drought, Land Use, and Novel Predation

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond Sep 1, 2015 you must submit a modification or new protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian

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Chapter 3: Modeling effects of disturbance across life history strategies of stream fishes

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Abstract

A central goal of population ecology is to establish linkages between life history strategy, disturbance, and population dynamics. Globally, disturbance events such as drought and invasive species have dramatically impacted stream fish populations and contributed to sharp declines in freshwater biodiversity. Here, we used RAMAS-Metapop to construct stage-based demographic metapopulation models for stream fishes with periodic, opportunistic, and equilibrium life history strategies and assessed their responses to disturbance scenarios that approximated the effects of invasion, drought, and the additive effects of both disturbances. Our models indicated that populations respond differentially to disturbance based on life history strategy. Equilibrium strategists were best able to deal with simulated invasion. Periodic strategists did well under lower levels of drought, whereas opportunistic strategists outperformed other life histories under extreme seasonal drought. When we modeled additive effects scenarios, these disturbances interacted synergistically, dramatically increasing terminal extinction risk for all three life history strategies. Modeling exercises that examine broad life history categories can help to answer fundamental ecological questions about the relationship between disturbance resilience and life history, as well as help managers to develop generalized conservation strategies when species-specific data are lacking. Our results indicate that life history strategy is a fundamental determinant of population trajectories, and that disturbances can interact synergistically to dramatically impact extinction outcomes.

Key Words

Life history, Metapopulation, Fish, Disturbance, Streams

Introduction

Many empirical and theoretical examinations of ecological systems strive to group organisms according to traits that describe their population trajectories. Previous work has classified organisms along continuums of life history strategies focused both on reproductive capacity (e.g., *r*- and *K*-selection) (Macarthur and Wilson, 1967; Pianka 1970), and survivorship (e.g., Van Valen 1973). These classifications can provide ecologists with a framework to examine organisms across ecological gradients irrespective of phylogenetic origin (Balon 1975). Because population-scale responses to environmental heterogeneity and ecological disturbance are driven by life history strategy (Van Winkle et al. 1993), examination of phenotypic convergences benefits both theoretical examinations of ecology, as well as management and conservation efforts (Balon et al 1977; Winemiller and Rose 1992).

Winemiller and Rose (1992) classified North American freshwater fishes into categories along a triangular continuum based on three life history traits (longevity, age at maturity, and fecundity). Within this general framework, three broad trait combinations were identified; periodic, opportunistic and equilibrium, with each endpoint of the generalized life history triangle representing a template for how a species might deal with a given disturbance event (Van Winkle et al. 1993). Periodic species are those with high fecundity, low parental care, and longer maturation times. These species can persist through sub-optimal environments and produce large egg clutches once conditions are more favorable (Winemiller 1995; Chesson 1984). Opportunistic species tend to be very highly fecund with short maturation times and can readily recolonize after disturbance events in a similar fashion to traditionally classified *r*-selected species (Diamond 1974). Finally, equilibrium species, like other *K* strategists (Pianka 1979), have low fecundity and long maturations, but high parental care and energy investment that allow them to outcompete other species when environments are relatively homogeneous

(Winemiller and Rose 1992). The adaptations many fish species have evolved to respond to disturbance fall somewhere within or between these specializations.

Life history strategy is an important predictor of how a species will respond to, and persist through, disturbance events (Van Winkle et al. 1993). Two common disturbances in stream systems, drought and invasive species, greatly influence population dynamics and evolutionary processes (Boulton 2003). Furthermore, these disturbances can be exacerbated by anthropogenic actions (Bond and Lake 2005). Indeed, the biota of highly anthropogenically-impacted systems in North America are among the most threatened globally (Jelks et al. 2008). Because life history mediates how biota respond to individual disturbances, a better understanding of how disturbances influence population dynamics of species with different life history strategies is fundamental to improving our capacity to predict the impacts of altered disturbance regimes and to the protection of aquatic biodiversity.

Drought is a natural phenomenon that affects systems on every continent and imposes a wide variety of environmental and ecological effects on stream fauna (Beche et al. 2009). In many headwater systems globally, (e.g., Ozark Highlands of the United States, Spain, Australia, South America, and Africa) streams tend to dry in the summer and early autumn and seasonal drought is a defining hydrological feature. Accordingly, drought is an important driver of population and community dynamics in these systems (Magoulick and Kobza 2003). While droughts can directly affect mortality as water availability decreases, aquatic ecosystems also undergo several physical, chemical, and hydrological changes during drought—many of which elicit biological responses (Lake 2003). Decreased water availability can lead to unfavorable abiotic conditions (i.e., higher temperatures, decreased dissolved oxygen levels) that directly influence vital rates (Kanno et al. 2015). Furthermore, diminished critical flows during droughts can impact reproductive success (Poff and Ward 1989). Drought can also lead to an increase in density-dependent population effects as individuals move into remaining waters (Matthews

1998) and drought-based increases in density can amplify the effect of biotic interactions and increase invasion susceptibility (Mitchell et al. 2006). Additionally, drought can severely limit habitat connectivity and disrupt metapopulation dynamics (Magoulick and Kobza 2003; Bond et al. 2015). However, many organisms in drought-prone environments have evolved adaptations to drought events based on their life history (Poff and Ward 1990; Townsend and Hildrew 1994). For example, periodic specialists tend to have longer life spans and can persist through predictable drought events, laying large clutches of eggs post-disturbance (Olden and Kennard 2010). Therefore, life history strategy should be considered in the management and conservation of fishes in drought-prone environments.

Invasive species can have significant detrimental ecological effects in freshwater ecosystems (Grabowska et al. 2010) and the environmental damage caused by invaders costs several billion dollars annually in the United States (Pimentel et al. 2005). Invaders have been implicated in the decline and extirpation of native fish species in a variety of freshwater systems (e.g., Winfield et al. 2011). Because many invaders directly compete with native species for similar resources, they can reduce the overall system carrying capacity (Sax et al. 2005). However, invaders can also alter the evolutionary pathways of native species by niche displacement, introgression, hybridization, predation, as well as extinction (Mooney and Cleland 2001). Furthermore, the relative effect of invaders might be amplified because of global climate change (Rahel and Olden 2008). However, the establishment and relative effect of invasive species is often dependent on the life history of both the invader and the native species (Allendorf and Lundquist 2003; Olden et al. 2006). For instance, equilibrium species tend to be superior competitors and can displace species that expend energy in other areas of niche space (Fox et al. 2006). Accordingly, additional examinations of life history strategy might be instructive to our understanding of invasion biology more generally.

While the environmental effects of drought and invasive species are both well documented, the effects of compounded disturbances still represent a significant gap in our understanding of freshwater ecology (Ormerod et al. 2010). Disturbances can interact synergistically or antagonistically, and management or conservation strategies that account for only one stressor might be insufficient to protect stream fauna and water resources (Christiansen et al. 2006). Drought can amplify biotic interactions like competition and predation due to crowding effects (Matthews 1998) and increase the relative effect that an invader might have on a native species. Furthermore, drought can also induce behavioral changes, including the loss of defensive or social behaviors, increasing the vulnerability of species to invaders (Fischer and Ohl 2005). Additionally, disturbance regimes including predictable drought events might facilitate biological invasions (Scoppetone et al. 2005).

Matrix population models (MPM) are a well-established tool that allow the examination of population dynamics based on life history parameters (Brook et al.2000). These models are age- or stage-structured and utilize survival and fecundity data to project populations through time (Leslie 1945; Akçakaya 2000). Additionally, MPM can be structured into a metapopulation framework to examine spatially-explicit population dynamics (Akçakaya and Root 2002). Notably, MPM allow researchers to develop population viability analyses (PVA) that have been used extensively in conservation strategies (Beissinger and Westphal 1998). Previous work has sought to develop MPM for many species examined in Winemiller and Rose (1992) (e.g., Velez-Espino et al 2005). However, MPM can be difficult to parameterize as species-specific life history data are often lacking or non-existent for many taxa (Akçakaya 2000).

In this study, we attempted to develop matrix-based metapopulation models that explore the population dynamics of stream fish with varying life histories. Our models examine representative fauna for each life history strategy of the Winemiller and Rose (1992) life history triangle. The models approximate scenarios involving seasonal drought, invasion, and the additive effects of both disturbances on these populations. In doing so, we hope to better understand how life history strategy can predict species reactions to disturbance as well as develop a framework that provides managers and conservationists with tools to develop PVA when species-specific life history data are unavailable.

Methods

Data Sources

We took vital rates of target species from established literature sources when available (i.e., Lehtien and Echelle 1979; Quist and Guy 2001; Spromberg and Birge 2005; Espinoa and Koops 2012; Carr et al. 2015). Additionally, we used the COMADRE animal matrix database to search for established matrices (Salguero-Gómez et al. 2015). Initial abundance, density estimates, and movement parameters were species-specific and taken from available literature (i.e., Munther 1970; Mundahl and Ingersoll 1989; Bovee et al 1994; Peterson and Kwak 1999; Smithson and Johnston 1999; Quist and Guy 2001, Dauwalter and Fisher 2007; Hodges and Magoulick 2011; Todd and Rabeni 1989). If we encountered more than one value for a parameter, we used the mean for continuous data and the median for discrete data (Velez-Espino et al. 2006).

Model Overview

We used RAMAS Metapop (Akçakaya and Root 2002) to construct demographic models for the three life histories in the Winemiller and Rose (1992) triangle (periodic, opportunistic, and equilibrium). Because life history and movement data are relatively scarce, we chose to incorporate data from multiple related species to fully parameterize our model. The periodic life history was represented by members of the genus *Campostoma* (*C. anomalum, C. spadiceum*). The opportunistic life history was represented by members of the genus *Notropis* (*N. boops, N. anogenus, N. percobromus, N. lutipinnis*). The equilibrium life history was parameterized by data representing the smallmouth bass, *Micropterus dolomieu*. All three of these genera co-occur in the Ozark Highlands of Arkansas, Missouri, and Oklahoma where seasonal drought is a prominent hydrological feature (Robison and Buchannan 2020; Hodges and Magoulick 2011). The models incorporate stochasticity by drawing from a lognormal distribution around the mean of the life history parameters at the beginning of each simulation.

For periodic and equilibrium species, models consisted of four demographic stages: juveniles, young adults, adults, and old adults. For periodic species: young adults are reproductively active, while old adults are not. For equilibrium species: young adults are not reproductively active, while old adults are (Winemiller and Rose 1993). We split adult stages to better account for differential age-based fecundity. In our model, opportunistic species mature rapidly and only have two demographic stages: juvenile and adult. In all models, juveniles are non-breeding and represent organisms from age 0 until maturity (Figure 1). Our models assume post-breeding status, meaning survival and reproduction probabilities are calculated after the breeding season.

The models integrate ceiling-type density dependence by incorporating carrying capacities for each subpopulation wherein population dynamics are only affected by density dependent factors once they exceed the carrying capacity, allowing for overcompensatory dynamics. While some fish species experience population regulation at low densities (Winemiller 2005), we chose to maintain the same density dependence across all life histories to facilitate comparability. We assume stable natural populations are relatively close to their carrying capacity, and thus quantify total carrying capacity as 105% of the field density of females (sensu Yule et al 2009). The metapopulation was split into subpopulations accounting for microhabitats within a typical stream reach. Each metapopulation consisted of a total of 30 subpopulations divided evenly among large (75 m^2), medium (50 m^2) and small habitats (25 m^2). Habitat sizes were placed systematically in order (large, medium, small) throughout the stream segment. Our extinction thresholds were defined as 5% of the carrying capacity of the metapopulation (sensu Yule et al., 2009). Each model was run for 100 years over 1000 iterations.

We assessed population viability by examining terminal extinction risk, median time to quasi-extinction, and metapopulation occupancy. Terminal extinction risk is the probability that total metapopulation abundance will fall below the extinction threshold by the end of 100 years. Median time to quasi-extinction is the time it takes any iteration to fall below the metapopulation extinction threshold. Metapopulation occupancy is defined as the number of extant subpopulations given 100 years (Akçakaya and Root, 2002).

Model Parameterization

Fecundity (F_i) was estimated to be the annual production of female offspring per adult female in stage class i. We assumed a 1:1 sex ratio for all species. Therefore:

$$F_i = (\text{clutch size} * \text{annual number of clutches})/2.$$

We defined P_i as the probability that an individual in stage class i survives to stage class $i+1$. Baseline survival probabilities were species specific. (Table 1)

The rate of fecundity (F_iP_i) is given as the product of survival probability (P_i) and fecundity (F_i) (Velez-Espino et al., 2006) since parents must persist through the previous stage classes to reproduce.

Subpopulation starting abundance was species- and stage-specific and based on densities found using percent frequency from size-frequency distributions. The models are spatially explicit, and subpopulations are placed using X and Y coordinates on a Cartesian plane. Based on the spacing of consecutive pool habitat units in streams inhabited by the focal species, each subpopulation was placed 30 meters longitudinally away from the previous subpopulation. We define dispersal as the probability of movement from one subpopulation to another after changes in survival and reproduction (Akçakaya and Root, 2002). We include a distance-function matrix that governs movement probabilities (M_{ij}) between populations using a distance decay function with an additional constraint on maximum dispersal distance (D_{max}). The distance decay function was:

$$M_{ij} = a * \exp(-D^{c}_{ij} / b), \text{ if } D < D_{max}$$

$$M_{ij} = 0, \text{ if } D > D_{max}$$

Where D is the total distance moved, a is the proportion of dispersing individuals, and b and c are functional constants. D_{max} and a were species-specific and representative of the life history group (Table 1), while b and c were constant across all models (we set them to 15.0 and 1, respectively). Movement was not influenced by density-dependent factors.

Sensitivity Analysis

We performed a sensitivity analysis by varying each vital rate (fecundity and survival) and movement parameter (*a* and *Dmax*) by ± 25% of the baseline while keeping the other parameters constant (Akçakaya, 2000). We then examined terminal extinction risk and took the absolute value of the high estimate minus the low estimate.

Drought and Invasion Scenarios

We modeled disturbance scenarios via parameter reductions intended to approximate conditions under common stream disturbances, seasonal drought and invasion. Drought has been shown to reduce both survival probabilities and fecundity in many fish species (Poff and Ward 1989; Kanno et al. 2015). To mimic the effects of intensified yearly seasonal drought, we reduced vital rates by 5%, 10%, and 15% for the length of the simulation. These reductions represent an estimated range of intensities for a given seasonal drought regime (Yarra and Magoulick 2019). To simulate invasive species, we similarly reduced species-specific carrying capacities. These invasion effects were modeled over a gradient of 10%, 20%, 30% and 40%

reductions to the baseline. We chose to model invasion this way because invasive species can compete for the same resources as native species, reducing species-specific carrying capacity (Sax et al. 2005; Keeler et al 2006; Julia et al. 2007). We also constructed an additive model that incorporates simultaneous disturbances from drought and invasion. To do this, we modeled each life history over a gradient of 10% reduction in carrying capacity and 5% reduction in vital rates, 20% reduction in carrying capacity and 10% reduction in vital rates, and 30% reduction in carrying capacity and 15% reduction in vital rates.

Results

Baseline scenarios

Baseline scenarios resulted in low terminal extinction risks for all species. Terminal extinction risk of the metapopulation was 4.4% for periodic species, 17.6% for opportunistic species and 2.3% for equilibrium species. For periodic species, 15.8% of subpopulations were expected to remain occupied after 100 years, with opportunistic and equilibrium species showing terminal occupancy rates of 9.4% and 12.7%, respectively. Periodic and equilibrium species did not fall below quasi-extinction thresholds throughout the 100-year simulation. However, opportunistic species had a median time to quasi-extinction of one year, indicating a population crash following the first time-step that stabilized as the simulation continued.

Sensitivity Analysis

Extinction risk was most sensitive to the juvenile survival parameter for every species (Figure 2). For opportunistic species, the second most sensitive parameter was adult fecundity. However, terminal extinction risk fell as fecundity was lowered. For equilibrium species, young adult survival was the second most sensitive parameter. The models were comparatively insensitive to changes in all other parameters (maximum effects <29%) (Figure 2).

Intensified seasonal drought

Reductions in vital rates due to drought led to an increased terminal extinction risk for all species (Figure 3). At 5% and 10% reductions, periodic species were the most robust while opportunistic species were the most vulnerable. However, at 15% reduction, this trend reversed, and opportunistic species had the lowest terminal extinction risk followed by periodic and equilibrium species. Across all reductions, opportunistic species had the fastest median time to quasi-extinction (Figure 3), followed by equilibrium and periodic species. Equilibrium species had the fewest occupied patches at all levels of reduction. While periodic species had more occupied patches at lower vital rate reductions, opportunistic species had the most occupied patches at 15% reductions (Figure 3)

Competitive effects of invasion

All species had increased terminal extinction risk for all levels of reduction in carrying capacity (Figure 4). Equilibrium species were the most resistant to invasion, followed by periodic and opportunistic. At low levels of reduction, periodic species had the slowest median time to quasi-extinction, followed by equilibrium and opportunistic species. Similarly, periodic species had the most occupied patches at low reductions, but equilibrium species had the most occupied patches at higher levels of reduction. All species suffered near total extinction at 40% reductions; however, equilibrium species had the slowest median time to quasi-extinction (Figure 4).

Additive effects

Additive effect scenarios caused dramatic increases to extinction risk for all species (Figure 5). While equilibrium species were the most robust under the first scenario (5% vital rate, 10% carrying capacity), followed by periodic and opportunistic, all three species were largely extinct under scenarios entailing additional reductions. Likewise, all species were expected to have less than 1 occupied subpopulation under 10/20% and 15/30% reduction scenarios. However, periodic species had a slower median time to quasi-extinction than both equilibrium and opportunistic species under all reduction scenarios (Figure 5). Additionally, the terminal extinction risk for periodic and equilibrium species under the first additive effect scenario (61.9% and 54.4%, respectively) was greater than the cumulative terminal extinction risks for the previous disturbance scenarios and baseline combined (57.2% and 42.7%, respectively).

Discussion

Our results largely supported the predictions of Winemiller and Rose (1992) in a theoretical framework. Life history strategy strongly influenced the effects of disturbances on fish population dynamics. The low terminal extinction risk for all species in baseline scenarios demonstrated that all three life history strategies are likely adequate for species persistence in systems with no disturbance. However, opportunistic species were the least stable and had the highest baseline terminal extinction risk. Like traditionally categorized *r*-selected species, opportunistic life histories can see dramatic fluctuations in population size due to rapid population growth and high turnover rates (Winemiller and Rose 1992). These factors can lead to decreased stability across the smaller geographic and temporal scales that our models approximated.

Across all life histories, extinction risk was most sensitive to changes in juvenile survival. Previous work has demonstrated the relative importance of juvenile survival to species persistence across a wide variety of teleosts (Sogard 1997). Indeed, many conservation efforts have centered on juvenile life stages (Crouse et al. 1987, Beck et al. 2001). However, conservation needs of juvenile stages could vary among life histories. For instance, opportunistic juveniles are highly susceptible to predation and might greatly benefit from increased refuge habitats; whereas equilibrium species would likely benefit from management strategies that better facilitate parental care (Winemiller and Rose 1992). Our models indicate that terminal extinction risk decreased with fecundity for opportunistic life histories, and that adult fecundity was also a highly sensitive parameter for these species. This is likely due to a release from competitive stress at the juvenile stage as density-dependent intraspecific competition levels fall (Vonesh and De la Cruz 2006). Furthermore, high levels of fecundity can cause rapid fluctuations in population growth rates and result in greater instability during the initial time steps in matrix population models (Cushing and Yicang 1994). These fluctuations lead to very low median times to quasi-extinction for opportunistic strategists across all scenarios. Because larval and juvenile population dynamics can have significant impacts on population viability (Sogard 1997), a better understanding of stage-specific dynamics is necessary to implement more effective conservation and management strategies (Rose et al. 2001). Though sensitivity analyses can provide valuable insight into what stages or ages are particularly sensitive to disturbance (Aberg et al. 2009), they can be difficult to interpret in taxa with lumped stages of varying duration (Lesnoff et al. 2003). Accordingly, model estimates could be greatly improved with more detailed data across all life histories (Rose et al 2001).

Though periodic species were the most sensitive to changes in dispersal ability, movement parameters (a, *Dmax*) were not influential for any life history strategy. Movement and dispersal capability are an important aspect of metapopulation dynamics and can be vital to population persistence in other aquatic species (Cowan and Sponagule 2009). Furthermore, dispersal in response to spatial heterogeneity can be a key component of life history. Our models incorporated spatial heterogeneity by varying subpopulation sizes and we found that life history influenced patch occupancy. However, our models explored relatively small spatial scales (approximately 1.5 km of a stream reach) and thus the relative influence of movement on population dynamics was likely diminished. Modelling efforts that focus on larger spatial scales might provide additional insight on how disturbance affects metapopulation dynamics across life history strategies.

Reduction of vital rates in our drought scenarios had differential impacts across life history strategies. At low levels of disturbance, periodic species had the lowest terminal extinction risk as well as the highest metapopulation occupancy. These species tend to be longer-lived with high fecundity that allows them to persist through disturbances and deliver larger clutch sizes to repopulate (Winemiller and Rose 1992) in a manner similar to Chesson's (1984) 'storage effect'. Previous examinations of freshwater fish species have shown that periodic strategists tend to do best in environments with predictable disturbance regimes (Olden and Kennard 2010). However, under high-intensity disturbance scenarios that can wipe out entire cohorts, opportunistic species tend to dominate (Warner and Chesson 1985; Olden and Kennard 2010). This trend was present in our models as well, with opportunistic species having the lowest extinction rates and occupying the greatest proportion of the metapopulation at the highest levels of vital rate reductions (15%). This is likely due to opportunistic strategists' very high fecundity and their ability to quickly repopulate in the absence of competitors (Winemiller and Rose 1992). Many *r*-selected species have been shown to be effective colonizers after local extinctions (Diamond 1974). Conversely, equilibrium species had the highest terminal extinction risk at 10% and 15% reductions. Equilibrium and other *K*-selected strategists often flourish in stable environments by outcompeting other species (Pianka 1979). However, this often leaves them unequipped to persist through disturbance events. Because life history strategies are an important predictor of drought resistance and resilience (Schlosser 1990; Lytle and Poff 2004), additional exploration of population dynamics, including the collection of previously sparse life-history data, is necessary.

Our models indicate that life history is an important predictor of invasion susceptibility or other factors that reduce carrying capacity. Under all reduction scenarios, equilibrium strategists were the most resistant to simulated invasion, while opportunistic strategists were the most susceptible. Previous work has demonstrated that growth rates (e.g., Lawton and Brown, 1986) and reproductive strategy (e.g., Sakai et al., 2001) of both native species and invaders can determine invasion success. Equilibrium species tend to be strong competitors (Winemiller and Rose 1992) and are often successful invaders in their own right (Vila-Gispert et al. 2005; Olden et al. 2006). Conversely, opportunistic species are more adept at dealing with abiotic disturbances but are often inferior competitors (Olden and Kennard 2010). Intuitively, these trends are mirrored in our results. Interestingly however, despite having higher terminal extinction risks than equilibrium species, periodic strategists had slower median times to quasi-extinction. Their life spans, coupled with high fecundity, might allow periodic species to persist longer when faced with a superior competitor. Alternatively, in patchy environments where deterministic extinction is inevitable, superior competitors tend to go extinct more quickly than inferior ones (Tilman et al. 1994). Periodic specialists might fall within a middle range that slows their extinction relative to equilibrium strategists via extinction debt. Though we chose reductions in carrying capacity as a proxy for competitive invaders, there are many natural and anthropogenic factors that can similarly reduce the carrying capacity of freshwater fishes (Cramer and Ackerman 2009). Additionally, carrying capacity is a determinant of natural population size and our initial population sizes similarly informed our system carrying capacity estimates. However, species with smaller population sizes have an inherently higher risk of extinction (Pimm 1991) and our models did not explicitly manipulate initial population size independently of carrying capacity reductions within each life history strategy. Our models reinforce previous findings that have shown that MPM can be useful tools in elucidating the relationship between life history strategy and invasion susceptibility (e.g., Govindarajulu et al. 2005). Accordingly, theoretical examinations of life history strategy, including the construction and parameterization of matrix models, remain relevant to conservation and management goals for many imperiled taxa.

All three life history strategies were highly susceptible to the additive effects of disturbance. While equilibrium strategists had the lowest terminal extinction risk, followed by periodic and opportunistic species, given 5% reduction in vital rates and 10% reductions in carrying capacity, all three life history strategies had a terminal extinction risk of nearly 100% at all other levels of reduction. Disturbances can act synergistically in stream systems (Christiansen et al. 2006) and our results seem to display some level of synergistic interaction. The terminal extinction risk for periodic and equilibrium species under our first additive effect scenario (61.9% and 54.4% respectively) is greater than the cumulative terminal extinction risks for the baseline, 5% vital rate reduction, and 10% carrying capacity reduction scenarios combined (57.2% and 42.7% respectively). Thus, our models indicate disturbances that reduce vital rates and carrying capacities have a greater effect on population dynamics when operating in tandem than each does individually. Drought can amplify the competitive effects of an invader through crowding effects (Matthews 1998; Magoulick and Kobza 2003) and disturbance regimes can facilitate invasions (Scoppetone et al. 2005). Additionally, anthropogenic climate change is expected to increase the relative frequency and severity of drought events and exacerbate the effects of biological invasions across numerous taxa (Hellmann et al. 2008). Accordingly, conservation and management schemes might be insufficient to protect stream biodiversity if they fail to account for multiple, simultaneous disturbances.

While our disturbance scenarios broadly examined the potential effects of drought and invasion, these disturbances are complex, and can affect life history parameters in ways not explored in our simulations. For example, our models assumed that the effects of invaders on carrying capacity were unaffected by disturbance, whereas the opposite may be true for some invaders, where their increased susceptibility to disturbance may facilitate coexistence (e.g. Closs and Lake, 1995). Because our disturbance scenarios consisted of specific parameter reductions, they could more generally apply to any disturbance that affects survival, reductions in carrying capacity, or combinations thereof. By presenting a generalizable framework that overcomes some of the inherent complexity of these systems, it may be possible to disentangle some of the underlying ecological processes that govern population responses to disturbance. More generalized models can help to ameliorate some of this complexity by facilitating interpretation of the ecology of these systems. Subsequent iterations can build upon these baselines in a stepwise, iterative fashion to incorporate increasing levels of complexity without sacrificing transparency or interpretability (Grimm and Railsback 2012).

Life history patterns seem repeatable even among distantly related taxa (Vila-Gispert et al. 2002). Accordingly, demographic models have been an effective tool in species conservation (Parker, 2000; Beissinger and McCullough 2002). In fishes, the life history classifications of Winemiller and Rose (1992) have been applied to previous demographic modeling exercises (e.g., Velez-Espino et al. 2006; Yen et al. 2013). However, the absence of adequate demographic data is one of the most pervasive barriers to the construction of demographic models (Akçakaya 2000; Salguero-Gómez et al. 2015). Modeling exercises that focus on life history strategy might alleviate some consequences of species-specific data scarcity. Here, our models reinforce the idea that life history strategy is an important predictor of disturbance response in stream fish populations. Furthermore, our models predict that disturbance events can interact synergistically to impact extinction outcomes. Our modelling approach can be applied to a wide variety of systems to examine disturbance regimes when other methods of examination are infeasible, as well as provide stakeholders with a tool to explore the effects of single- and multi-disturbance regimes on stream fishes and develop appropriate management and conservation strategies.

Acknowledgements

Partial funding for this experiment was provided by the Arkansas Game and Fish Commission and United States Geological Survey. We thank J.D. Willson, Donald DeAngelis, and two anonymous reviewers. Their comments greatly improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Appendices

Tables

Table 1: Baseline model parameter estimates for each life history

Category	Parameter	Estimate	Primary Source
Opportunistic			
Survival probabilities	Juvenile	0.02	Carr et al. 2015
	Adult	0.22	Carr et al. 2015
Fecundity	Adult	137	Carr et al. 2015
Movement	*a*	0.5	Hodges and Magoulick 2011
	D*max*	105.3 m	Todd and Rabeni 1989
Abundance	Starting Abundance	2480	Hodges and Magoulick 2011
Periodic			
Survival probabilities	Juvenile	0.025	Quist and Guy 2001
	Young Adult	0.6	Quist and Guy 2001
	Adult	0.1	Quist and Guy 2001
	Old Adult	0.02	Quist and Guy 2001
Fecundity	Young Adult	64.26	Winemiller and Rose 1992
	Adult	16.065	Winemiller and Rose 1992
Movement	a	0.6	Hodges and Magoulick 2011
	D*max*	135 m	Mundahl and Ingersoll 1990
Abundance	Starting Abundance	1860	Mundahl and Ingersoll 1990
Equilibrium			
Survival probabilities	Juvenile	0.17	Spromberg and Birge 2005
	Young Adult	0.3	Spromberg and Birge 2005
	Adult	0.4	Spromberg and Birge 2005
	Old Adult	0.15	Spromberg and Birge 2005
Fecundity	Adult	25	Spromberg and Birge 2005
	Old Adult	187.5	Spromberg and Birge 2005
Movement	a	0.24	Munther 1970
	D*max*	120 m	Munther 1970
Abundance	Starting Abundance	1200	Dauwalter and Fisher 2007

Figures

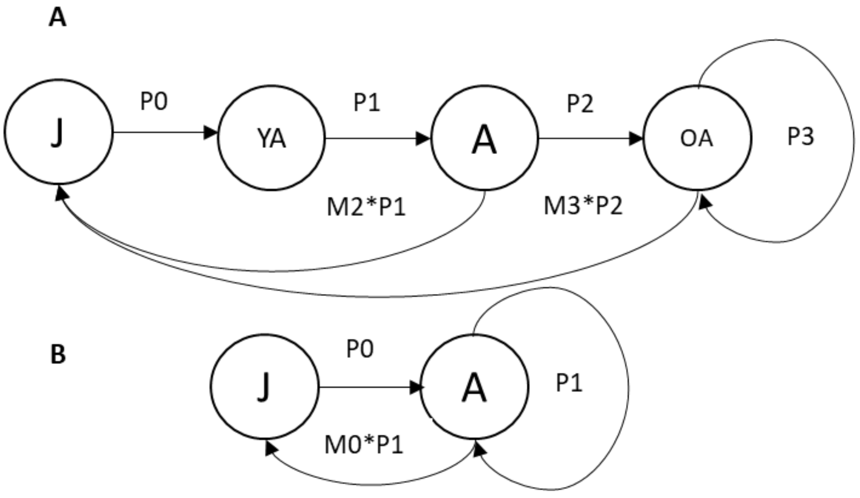

Figure 1: Generalized life cycle for A) Periodic and Equilibrium life histories and B) Opportunistic life histories. The life cycle is divided into 4 stages for Periodic and Equilibrium species: juveniles (J), young adults (YA), adults (A), and old adults (OA). The life cycle is divided into two stages for Opportunistic life histories: juveniles and adults. The circles represent life-history stages, and the arrows represent transitions between stages. M denotes stage transition probabilities and P represents fecundity. Stages not connected by an arrow have a zero entry in the transition matrix.

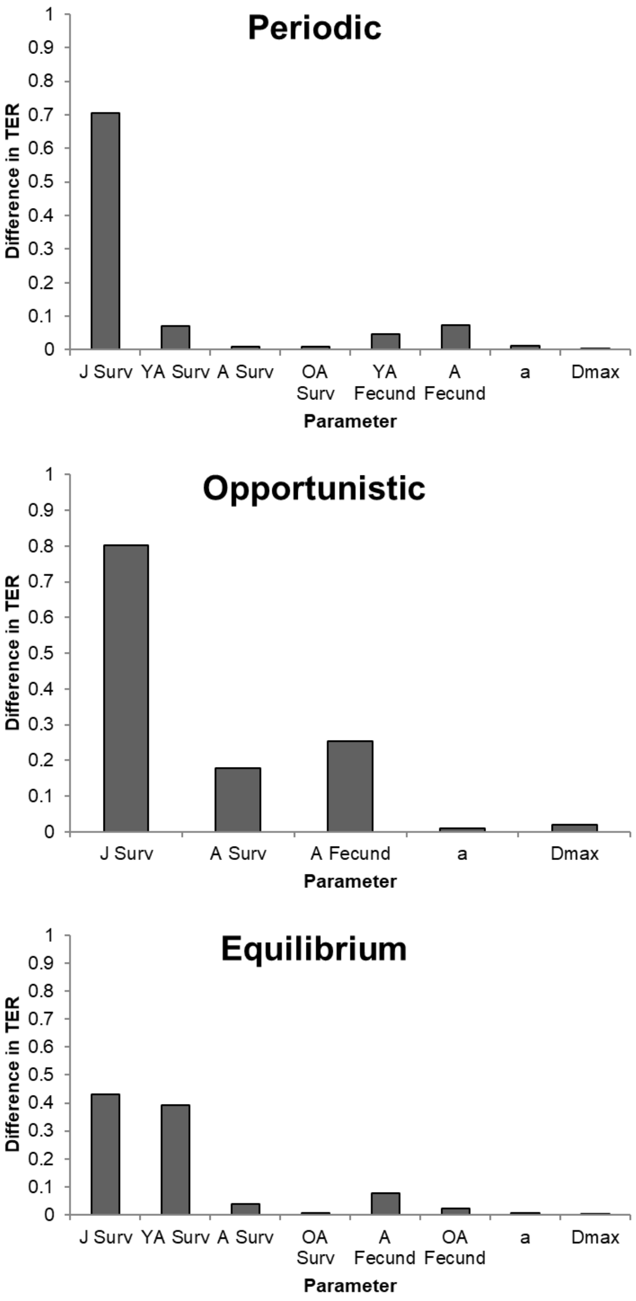

Figure 2: Sensitivity analysis derived from differences in terminal extinction risk (TER) between high and low parameter values for each vital rate (survival, fecundity) for Periodic species (top), Opportunistic species (middle) and Equilibrium species (bottom). Juvenile (J), Young Adult (YA), Adult, (A), Old Adult (OA), Maximum dispersal distance (D_{max}), the proportion of dispersing individuals (a)

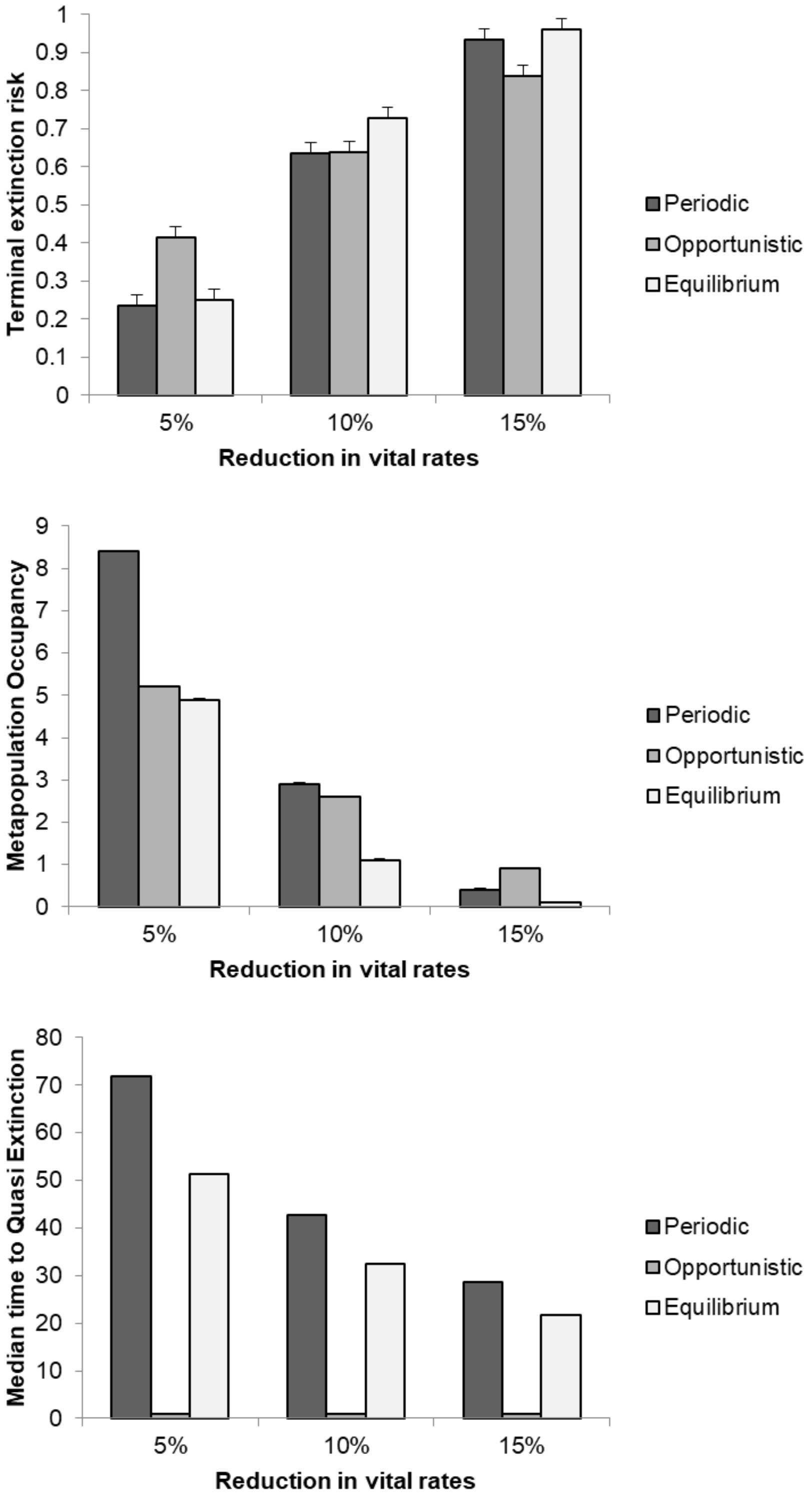

Figure 3: Terminal extinction risk (probablity, top), metapopulation occupancy (number of extant patches, middle), and median time to quasi-extinction (years, bottom) for all life histories given reductions in vital rates due to drought. Error bars indicate 95% confidence intervals.

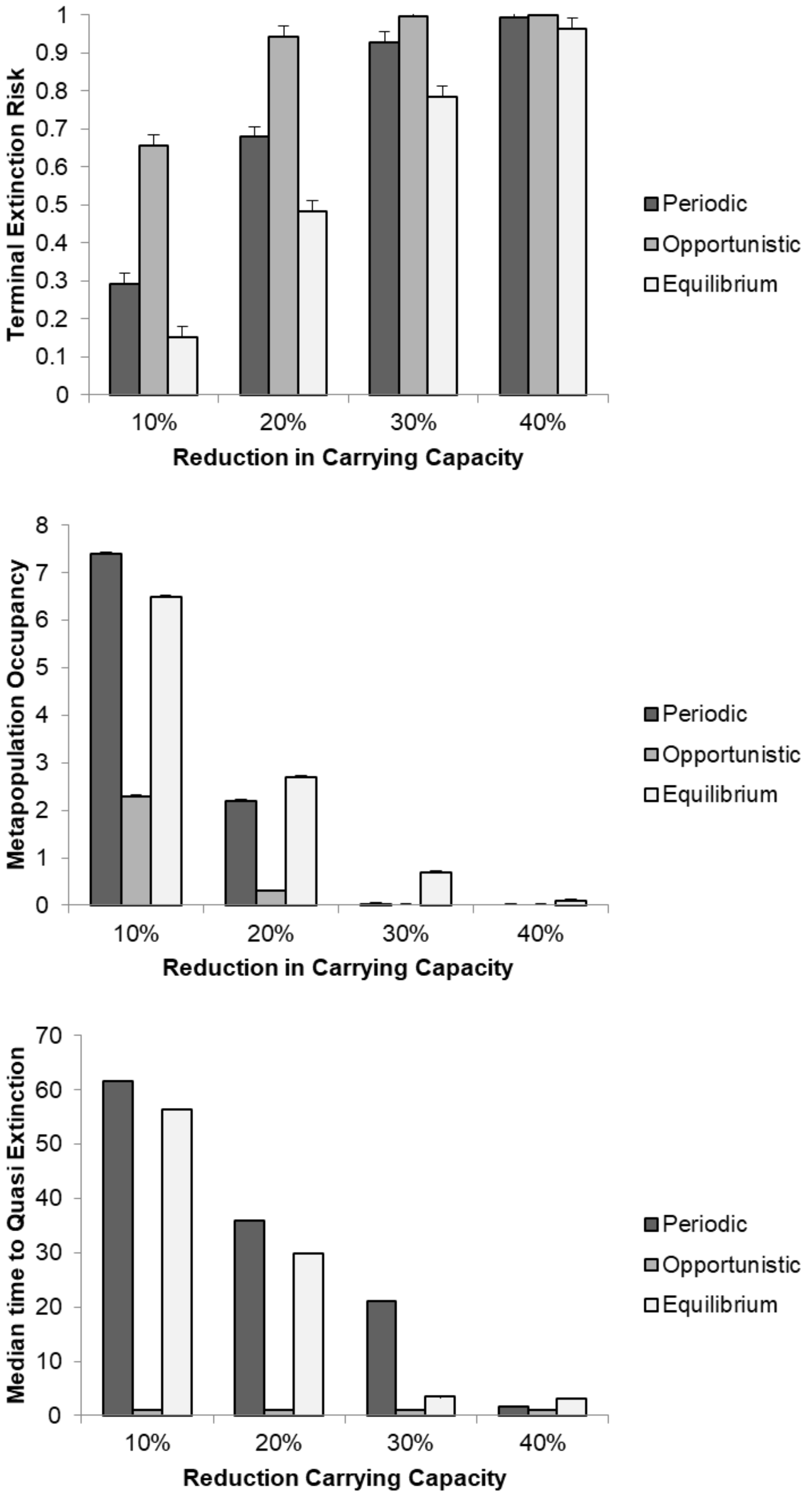

Figure 4: Terminal extinction risk (probablity, top), metapopulation occupancy (number of extant patches, middle), and median time to quasi-extinction (years, bottom) for all life histories given reductions in carrying capacities due to invasion. Error bars indicate 95% confidence intervals.

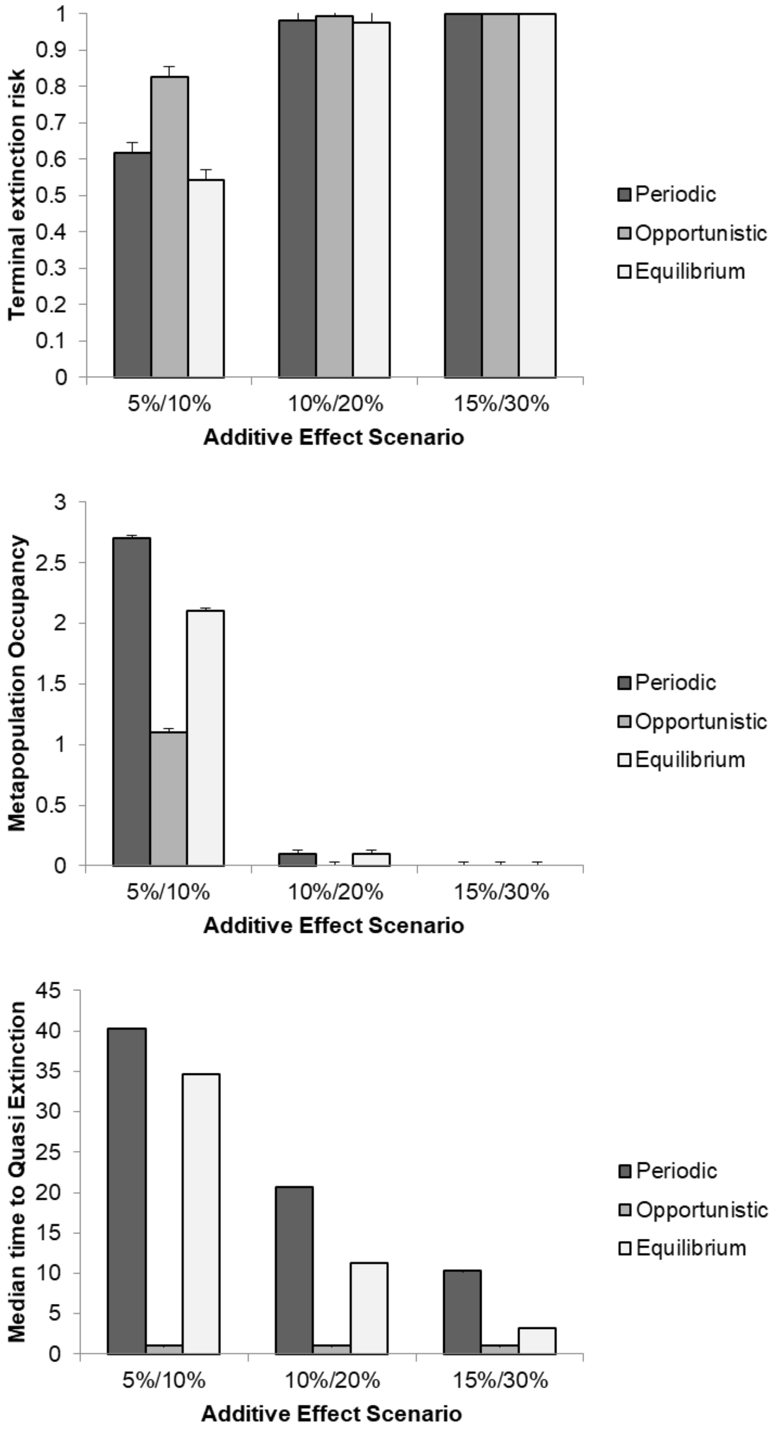

Figure 5: Terminal extinction risk (probablity, top), metapopulation occupancy (number of extant patches, middle), and median time to quasi-extinction (years, bottom) for all life histories given reductions in vital rates and carrying capacities in our additive effects scenarios. Error bars indicate 95% confidence intervals.

Conclusion

The results of this dissertation suggest that individual stressors can have far-reaching effects on multiple aspects of stream communities, and that combined stressors can act in both additive and antagonistic ways. However, we found that these interactions are context- and scale-dependent. The same stressor pairings interacted additively on one portion of the ecosystem, and antagonistically on another. Additionally, we found that while stressors might show no evidence of interaction on limited geographic or temporal scales, examination or modelling efforts focused on broader scales might indicate the presence of interactive effects.

We found that drought affects many aspects of benthic communities, including periphyton and macroinvertebrates. However, the effect of drought can vary by habitat type (e.g., riffle vs pool)(Magoulick and Kobza 2003). In shallow habitats, drought negatively impacted many aspects of benthic community structure and functioning. Conversely, pool habitats showed more mixed effects. Because drought increases the density of biota, algal biomass was increased when density-dependent predation pressure on grazers was increased during drought. Additionally, herbivory can increase chlorophyll concentrations when grazers remove senescent cells (Welch et al.1997). While we did not find that drought negatively impacted many fish and crayfish species in our experimental studies, our models that explored greater geographic and temporal scales showed that drought can negatively impact many fish species. However, the relative impact of drought was dependent on life history strategy—with high levels of drought favoring species capable of rapid reproduction following a disturbance event (i.e, opportunistic species). All of our experimental focal species (longear sunfish, central stoneroller, ringed crayfish, and smallmouth bass) co-occur naturally in the Ozark Highlands (Robison and Buchannan 2020). As streams in this system are prone to seasonal drying and desiccation, it is likely that these species are relatively drought adapted (Magoulick and Kobza 2003). However, the effectiveness of these adaptations might be diminished if drought events are intensified over longer time scales like those approximated by our models (Bond et al. 2008).

Nutrient inputs can cause bottom-up effects that destabilize food webs (Power 1992), and nutrient treatments impacted several portions of the community in our experiments. The nutrient concentrations in our experimental setup were designed to mimic agriculturally-polluted streams (Evans-White et al. 2009), and we saw increases in algal metrics at these levels. As crayfish are omnivores, and impact multiple portions of the food web (Momot 1995), nutrient inputs also increased crayfish growth rates. Conversely, nutrient pollution negatively affected survivorship of sunfish—likely by decreasing available dissolved oxygen. We also found that drought offset some negative effects of nutrient pollution on longear sunfish and acted additively with nutrient inputs to increase periphyton variables in deep habitats. The suppression of chironomids by increased predation pressures during drought coupled with the net increase in photosynthetic algae resulting from nutrient additions increased basal resources. This increase in resource availability positively affected longear sunfish survivorship and offset the decreased survival associated with nutrient treatments. While these effects benefited fish and crayfish species in our study, previous work has shown that drought and nutrient pollution might interact synergistically to negatively influence population dynamics (Lake 2003). However, negative effects of nutrient enrichment tend to be more influential over longer time-scales than our experiment examined (Donohue et al. 2009, Romero et al 2019).

In our experimental study, we sought to compare a native apex predator, the smallmouth bass, with a potential invader, the largemouth bass. As largemouth bass have higher energetic requirements (Anderson 1984), we hypothesized that their increased predatory pressures would have greater impacts on lower trophic levels than the smallmouth. While the bass-stoneroller-periphyton trophic link has been documented in stream systems (Power et al. 1988), we did not observe significant differences in their top-down pressures as both bass species nearly eradicated stonerollers from our experiment. One potential aspect of predation that our study did not account for is the speed of consumption of prey items. While both species eradicated stonerollers from the experimental tanks, it is possible that smallmouth and largemouth bass might have consumed stonerollers at different rates because of their differential energy requirements. Our models focused on the effects of a potential competitive invader and found that life history is an important predictor of invasion susceptibility. Under all invasion scenarios, equilibrium strategists were the most resistant to invasion, while opportunistic strategists were the most susceptible. In patchy environments where localized extinction is inevitable (like a severely-impacted drought system), superior competitors—like equilibrium strategists—tend to go extinct more quickly than species that specialize in disturbance resistance or resilience (Tilman et al. 1994). Additionally, our models found that the relative effect of invasive species was increased during droughts, and that these stressors acted synergistically to increase terminal extinction risk.

This dissertation highlights the complexity of stressors in stream systems. Throughout our experimental and modeling exercises, we saw varied effects of drought, nutrients, and invasive species effects on stream communities. In addition to single-stressor effects, these disturbances interacted in several surprising ways. However, these interactions were varied, and the same stressor pairings can produce multiple types of interactions—or only interact in certain contexts. Anthropogenic degradation of aquatic systems is likely to continue to increase, and the effects of drought, nutrient pollution, and invasive species are likely to be compounded in the future. Furthermore, as human population and resource continues to increase, it is increasingly likely that these stressors will co-occur. This work emphasizes that our understanding of individual stressors might not adequately inform our knowledge of multi-stressor systems. As many of our management or conservation strategies incorporate only one stressor, they might be inadequate to conserve aquatic resources. Accordingly, more work must be done to disentangle the effects of multiple stressors in stream systems. Stressor pairings not presented in this dissertation (i.e., nutrient pollution and invasive species) or additional stressors influencing stream communities (e.g., temperature, flooding, contaminants) remain fertile ground for future exploration. Finally, this dissertation demonstrates that stressor pairings might produce different outcomes over varying geographic or temporal scales, and that life history is an important determinant of stressor response. Accordingly, studies that examine stressor mechanisms at a variety of scales using taxa representing multiple life history strategies remain warranted.

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