

ORIGINAL ARTICLE

Freshwater mussels increase survival of largemouth bass (*Micropterus salmoides*) in drying pools

Traci P. DuBose¹  | Kathryn Ashford^{1,2} | Caryn C. Vaughn¹ 

¹Oklahoma Biological Survey, Department of Biology, University of Oklahoma, Norman, OK, USA

²School of Visual Arts, University of Oklahoma, Norman, OK, USA

Correspondence

Traci P. DuBose, Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK 73019, USA.
Email: tracipopejoy@ou.edu

Funding information

University of Oklahoma; National Science Foundation Division of Environmental Biology, Grant/Award Number: 1457542

Abstract

Between global climate change and anthropogenic water needs, freshwater systems are becoming more intermittent, stressing organisms adapted to perennial waters. Drought-induced intermittency concentrates aquatic organisms into drying pools. These pools represent refugia from desiccation but apply other stressors, such as extreme temperatures and increased competition for dwindling resources. In the Southern United States, fishes and freshwater mussels are often concentrated together in drying pools during seasonal, summer droughts. This can result in increased competition for food among invertivorous fish, but also increased food abundance for these fish because mussels increase macroinvertebrate abundance. Further, since mussels require fish as hosts for their ectoparasitic larval phase, glochidia, competition with their host during this biologically active time is detrimental to mussels. We conducted an experiment to examine the effects of freshwater mussels on trophic resources and fish survival in drying pools. We stocked mesocosms with juvenile largemouth bass that were infected or uninfected with glochidia and tracked abiotic conditions, trophic resources and fish survival for 10 days. We found that fish survived longer in the presence of adult mussels, regardless of their infection status. We suspect that prey items supplemented by adult freshwater mussels increased the survival of fish. Thus, the presence of adult mussels and the resources that increase in their presence potentially mitigate stress to fish in “ecological crunch times.” By conserving mussels, fish populations might withstand droughts more easily.

KEYWORDS

drought, ectoparasite, food web, intermittent stream, trophic facilitation, unionid

1 | INTRODUCTION

Extreme hydro-meteorological events such as droughts and heat-waves are becoming more frequent, more intense and more persistent in many parts of the world (Mellilo, Richmond, & Yohe, 2013). Streams in the southern Great Plains are projected to experience greater drought magnitude and frequency due to increased evapotranspiration and shifts in precipitation patterns (Datry, Larned, & Tockner, 2014; Naumann et al., 2018; Woodward, Perkins, & Brown, 2010). As precipitation becomes scarce, water levels decrease in

runoff dominated rivers. Rivers may become intermittent, consisting of series of isolated pools separated by dry riffles. These isolated pools become essential refugia for aquatic organisms that cannot aestivate, such as fishes (Lytle & Poff, 2004; Magoulick & Kobza, 2003; Pires, Pires, Collares-Pereira, & Magalhaes, 2010). However, drying pools are often subjected to increased abiotic extremes: high temperatures during the day and low oxygen at night (Mosley, 2015). Decreased nutrient inputs to these pools can shift the microbial regime from heterotrophic to autotrophic (Dahm, Baker, Moore, & Thibault, 2003). This shift can be exacerbated by increased solar

radiation and decreased flow, eventually culminating in algal blooms and associated drops in oxygen concentration at night (Mosley, 2015). These abiotic stressors impact fish physiology (Whitney et al., 2016), can force fish to enter an “ecological crunch” where resource competition is intense (Magoulick & Kobza, 2003; Weins, 1977) and expose fish to increased predation from other fish species (Harvey, 1991; Schlosser, 1987) and terrestrial predators (Gagnon, Golladay, Michener, & Freeman, 2004; Power, 1984; Wolff, Taylor, Heske, & Schooley, 2016). Small fish can often outlast larger, predaceous fish in isolated pools due to lower oxygen demand, but are subjected to higher predation pressure in larger refuge pools (Magoulick & Kobza, 2003). Thus, drought imposes both abiotic and biotic stressors on resident fishes (Lennox, Crook, Moyle, Struthers, & Cooke, 2019; Matthews & Marsh-Matthews, 2003).

Rivers in the Southeastern United States are known for their high fish and freshwater mussel biodiversity. Mussel larvae (glochidia) are obligate ectoparasites on fish (Barnhart, Haag, & Roston, 2008; Haag, 2012), and there is a strong positive relationship between mussel and fish diversity (Vaughn & Taylor, 2000). Mussels form dense, multispecies aggregations (mussel beds) in river reaches that are hydrologically stable (Sansom, Bennett, Atkinson, & Vaughn, 2018; Strayer, 1999), and these are often areas that become pool refugia as rivers dry. Thus, during droughts fishes are likely to be stranded in isolated pools with mussels. Mussels are ecosystem engineers that alter the benthic and water column boundary (Sansom, Atkinson, & Bennett, 2017). They increase benthic heterogeneity through their burrowing and create stable, heterogeneous habitat with their shells (Bódis, Tóth, Szekeres, Borza, & Sousa, 2014; Gutierrez, Jones, Strayer, & Iribarne, 2003) that are used as flow refugia by both insects and fishes (Hopper et al., in press). They connect the water column and stream substrate through their filter feeding, which reduces stream turbidity and repackages water column particles into discrete benthic packages (through their faeces and pseudofaeces; Strayer, 2014; Vaughn, Nichols, & Spooner, 2008). As such, mussels increase benthic resources such as algae and macroinvertebrates (Atkinson, Vaughn, Forshay, & Cooper, 2013; Spooner & Vaughn, 2006; Vaughn & Spooner, 2006). As mussel effects are strongest when water volumes are low, they are especially strong during droughts or typical summer conditions in many Southern U.S. rivers (Atkinson & Vaughn, 2015; Vaughn, Spooner, & Galbraith, 2007). Thus, the presence of adult freshwater mussels is likely beneficial to fish refuges.

Many host symbiotic relationships are only beneficial to both organisms during times of stress; otherwise, the dependent organism is considered parasitic on the host (Stachowicz, 2001). Fishes likely benefit from feeding on adult mussel-subsidised resources during low flow (Limm & Power, 2011), but also suffer costs from being parasitised by mussel larvae. Parasitised fish lose body volume, exhibit slower reaction to predator presence and change their feeding strategies (Crane, Fritts, Mathis, Lisek, & Barnhart, 2011; Filipsson et al., 2018). Heavily infected fish also suffer a respiratory burden that alters ventilation rates (Filipsson et al., 2018; Thomas, Taylor, & Garcia de Leaniz, 2013). Heavy glochidial loads can kill infected fish through

asphyxia and lesions on the gill tissues (Howerth & Keller, 2006). For some mussels, the glochidial infection period is highest in summer and overlaps with low-water conditions (Culp, Haag, Arrington, & Kennedy, 2011; Gates, Vaughn, & Julian, 2015); thus, infection may decrease fish survival in drought conditions. While adult mussels compete with fishes for oxygen, they may also subsidise prey for invertivorous fishes by increasing macroinvertebrate abundance (Vaughn et al., 2008). By bolstering the survival of freshwater fishes in drying streams, adult mussels potentially improve their reproduction potential for the following season. Most research investigating the trophic relationship between fishes and mussels investigate costs associated with glochidial parasitism and ignore benefits provided by adult mussels. We suspect that what has been defined as a parasitic relationship between freshwater mussel and fishes might be conditionally mutualistic.

We conducted an experiment to examine the effects of freshwater mussels on trophic resources and fish survival in drying pools. We stocked mesocosms with infected and uninfected juvenile largemouth bass and tracked abiotic conditions, trophic resources and fish survival for 10 days. We predicted that, while both adult freshwater mussels and glochidia reduce the amount of oxygen available to fish, adult freshwater mussels increase prey (macroinvertebrates) for fish and thus increase fish survival in drying pools.

2 | METHODS

2.1 | Experimental design

We conducted the experiment in 18, ~950 L circular tanks (hereafter “mesocosms”) that mimicked drying pools. Mesocosms were spaced ~2 m apart in a field at the University of Oklahoma Biological Station in Kingston, OK. Each mesocosm was lined with 15 cm of gravel (1:1 ratio of 10 and 38 mm diameter) and filled with ~635 L water. We filled the mesocosms in early May 2018 to allow for algal and macroinvertebrate colonisation from a nearby reservoir (Lake Texoma, 350 m distance), added mussels to the mesocosms on May 30 and added fish on June 18 (day 0). We added mussels to the mesocosms before adding fish to establish mussel bed conditions, such as differences in algal and invertebrate abundance. We aerated the mesocosms for the entire experiment to avoid night-time hypoxia that would have killed fish. During the experiment, mesocosms were always covered with shade cloth to prevent fish from escaping.

We had 9 mussel treatment mesocosms and 9 no-mussel control mesocosms. Mussel mesocosms contained 31 individual mussels (a density of 11.9 mussels/m²) that represented a natural community typical for the region (13 mucket *Actinonaias ligamentina* (Lamarck, 1819), 9 pimpleback *Cyclonaias pustulosa* (Lea, 1831), 5 threeridge *Amblema plicata* (Say, 1817), 2 pistolgrip *Tritogonia verucosa* (Rafinesque, 1820), 1 plain pocketbook *Lampsilis cardium* (Rafinesque, 1820) and 1 bankclimber *Plectomerus dombeyanus* (Valenciennes, 1827) (Atkinson, Julian, & Vaughn, 2012; Williams et al., 2017). We used juvenile, largemouth bass *Micropterus salmoides* (Lacepède, 1802) as our fish treatment. Largemouth bass were the

best fish species for this experiment because they are propagated, hosts for common mussel species, and have a month-long glochidial encystment period (Draxler et al., 2006). We wanted propagated fish to ensure fish did not have any prior glochidial infections, as subsequent infections decrease the success of glochidial attachment and metamorphosis (Rogers & Dimock, 2003). We chose juveniles because they exhibit the highest growth rate. We purchased largemouth bass “fingerlings” from the Peoria Tribe of Indians Aquatic Facility. We infected half of the fish with *Lampsilis cardium* glochidia following Patterson et al. (2018). We kept the infection density low to mimic natural infection (Kennedy, Pugh, Culp, & Benke, 2007; Patterson et al., 2018); fish in our experiment had an average of 7 glochidia on their gills ($SD = 6$ glochidia). We infected, weighed and measured (standard length) fish before adding them to the mesocosms on 18 June 2018 (day 0). Each mesocosm contained 5 infected fish and 5 noninfected fish for a density of 2.66 fish/m². We grouped fish by size to reduce cannibalism but randomly distributed the groups among mussel and control treatments. Fish had a mean weight of 14.7 g ($SD = 8.6$ g) and mean standard length of 95.0 mm ($SD = 15.9$ mm).

We monitored water temperature on an hourly basis in a random subset of mesocosms (HOBO UA-002-08 Pendants). We measured dissolved oxygen, conductivity and temperature at midday on experiment days -1 and 11 with a HACH HQ40d multiple parameter metre.

2.2 | Response variables

We measured response variables prior to adding fish (day -1, June 17) and on day 11 (June 28). Prior to the experiment, we placed 6 clay tiles (7.6 cm²) with an attached fritted glass disc (27.5 mm²) on the sediment surface in each mesocosm to allow benthic algal colonisation. On sampling days, two discs were removed and frozen. We sampled water column algae by filtering ~1 L (mean = 926 ml, $SD = 78$) of water through a microfiber filter (Grade F; 1.6 µm pore size) and freezing the filter. For both benthic and suspended algae, chlorophyll *a* was later cold-extracted with the acetone method and analysed spectrophotometrically (ASTM, 2012).

Prior to the experiment, six strawberry baskets (6 cm deep, 100 cm² surface area) were buried flush with the sediment in each mesocosm and allowed to be colonised by macroinvertebrates. On each sampling day, we removed three baskets and placed them in a 20-L bucket filled with clean water to create a slurry. We then washed the slurry through a 246 µm sieve and collected the macroinvertebrates (Bertrand & Gido, 2007). We also sampled invertebrates in the water column by pulling a plankton net (~153 µm mesh, 8 cm diameter) around a 5.4 m circumference circle in each mesocosm. All invertebrates were preserved in 70% ethanol. Benthic invertebrates were identified to family, enumerated and their length measured. We then used published length-dry weight equations to estimate macroinvertebrate biomass from density data (Benke, Huryn, Smock, & Wallace, 1999; Eckblad, 1971; Giustini, Miccoli, Luca, & Cicolani, 2008; Johnston & Cunjak, 1999; Miserendino,

2001; Obaza & Ruehl, 2013; Stoffels, Karbe, & Paterson, 2003). We took three subsamples from each water column sample to quantify zooplankton abundance (Lind, 1979).

We monitored mesocosms daily and removed dead fish when they were found. We identified the fish based on mesocosm-specific fin clips, took postmortem standard length and weight measures, and froze the specimens. After eleven days, 91% of the fish had died and the experiment ended. We later verified the fin clip identification and date of death, and quantified the glochidia on infected fish by excising all gill tissue and counting glochidia under a microscope.

2.3 | Statistical analyses

We used mixed linear models to test for differences among benthic and water column algal and macroinvertebrate abundance and biomass based on the fixed factor (mussel treatment), the fixed continuous variable (sampling day) and a random intercept accounting for mesocosm identity (R package *lme4*; Bates, Maechler, Bolker, & Walker, 2015; R Core Team, 2019). To assure these models met the assumption that residuals are normally distributed, we log₁₀ transformed benthic macroinvertebrate abundance, benthic macroinvertebrate biomass density, water column invertebrate density and water column invertebrate biomass density. We conducted a type III ANOVA with Satterthwaite's method to obtain *p*-values for all models (R package *lmerTest*; Kuznetsova, Brockhoff, & Christensen, 2017).

To determine whether mussels increased the survival of fish, we calculated Kaplan–Meier survival probabilities for the fish in each mesocosm (Christensen, 1987; Therneau & Grambsch, 2000). The Kaplan–Meier survival function estimator is a nonparametric statistic used to predict the probability of survival after a time, given knowledge of multiple observations status (alive/dead) and time of last observation. We excluded some fish from this data set; two fish were unaccounted for (suspected cannibalism among the fish) and six died the first night of the experiment and were replaced immediately. We completed two Cox proportional hazards regressions to evaluate the relationship between the Kaplan–Meier survival curve and our independent variables (mesocosm treatment and infection status) using the *coxph* function of the *survival* package in R (Therneau, 2015). When interpreting these models, β values relay the magnitude of a variable's correlation with survival; negative β values indicate increased survival. Hazard ratios greater than one represent an increase in the probability of death. All statistical analyses were conducted with R Core software version 3.5.3 (R Core Team, 2019).

3 | RESULTS

Our experiment successfully replicated the high temperatures typically found in drying streams in the Southern United States. During the experiment, the water temperature in the mesocosms ranged from 22.1 to 35.2°C with an average of 29°C and daily ranges up

TABLE 1 Mean (standard deviation) of ecosystem parameters and response variables measured prior to (day -1) and at the end (day 11) of the experiment

Treatment	Day	Physical-chemical parameters			Primary production		Fish	
		Temperature °C	Conductivity $\mu\text{S}/\text{cm}$	DO mg/L	Water column chlorophyll <i>a</i> $\mu\text{g}/\text{L}$	Benthic chlorophyll <i>a</i> $\mu\text{g}/\text{cm}^2$	Standard length mm	Wet weight g/m^2
Mussel	-1	27 (0.3)	347 (14)	7.47 (0.22)	3.69 (2.3)	3.91 (1.0)	95.2 (13.9)	40.3 (22.9)
	11	31 (0.7)	379 (60)	9.93 (2.21)	5.55 (3.1)	4.59 (1.5)	93.9 (17.4)	
Control	-1	27.1 (0.2)	345 (15)	7.36 (0.19)	6.81 (5.3)	2.19 (1.9)	95.3 (9.9)	40.5 (13.9)
	11	31.2 (0.6)	385 (59)	9.81 (1.34)	13.82 (16.6)	4.76 (2.7)	94.5 (14.7)	

to 6.5°C. Temperature, conductivity and dissolved oxygen increased and became more variable as the experiment progressed. Water column chlorophyll *a* concentrations were not significantly different between treatments ($F_{1,14} = 2.67, p = .12$) or between weeks ($F_{1,14} = 3.04, p = .10$). Benthic chlorophyll *a* concentration increased in the second week ($F_{1,16} = 11.45, p = .004$) but was not significantly different between treatments ($F_{1,16} = 0.82, p = .34$; Table 1).

Benthic macroinvertebrate abundance was not significantly different between treatments ($F_{1,16} = 0.12, p = .74$), but decreased significantly over time, particularly in control treatments ($F_{1,17} = 13.79, p = .002$; Figure 1a). Benthic macroinvertebrate biomass was not significantly different between treatments ($F_{1,16} = 0.42, p = .53$). Benthic macroinvertebrate biomass decreased mostly in control treatments but the relationship between biomass and time was marginally significant ($F_{1,17} = 3.93, p = .06$). Over the course of the experiment, benthic macroinvertebrates decreased in abundance and biomass in control tanks, though average individual invertebrate size increased (from a median length of 3.1–3.9 mm). In contrast, benthic macroinvertebrates had a stable abundance and biomass in mussel treatments, but were slightly smaller at the end of the experiment (from a median length of 3.4–3.1 mm). Water column invertebrates were primarily zooplankton (Cladocera), nonbiting midges (*Chironomidae*) and the predatory midge, *Chaoborus*. *Chironomidae* were likely dislodged during benthic sampling and do not represent invertebrate prey from the water column; as such, we excluded them from the analysis. Zooplankton density and biomass decreased in control and increased in mussel mesocosms during the experiment, while *Chaoborus* decreased over time in both treatments (Figure 2a,b). Considering all water column invertebrates (both zooplankton and larger invertebrates), there was not a significant difference between water column macroinvertebrate density in either treatment ($F_{1,16} = 0.004, p = .95$) or between days ($F_{1,17} = 0.14, p = .72$). There was not a significant difference between the water column invertebrate biomass between treatments ($F_{1,14} = 0.42, p = .53$) or between days ($F_{1,14} = 0.002, p = .96$).

Postmortem standard length and weight were similar among the treatments (Table 1). There was not a significant difference in the fish postmortem weight ($F_{1,16} = 0.0003, p = .98$) or postmortem standard length ($F_{1,16} = 0.0005, p = .98$). Fish residing in the mussel mesocosms had a mean weight change of -0.16 g ($SD = 2$) while fish in the control treatments had a mean weight change of 0.42 g ($SD = 2$). This

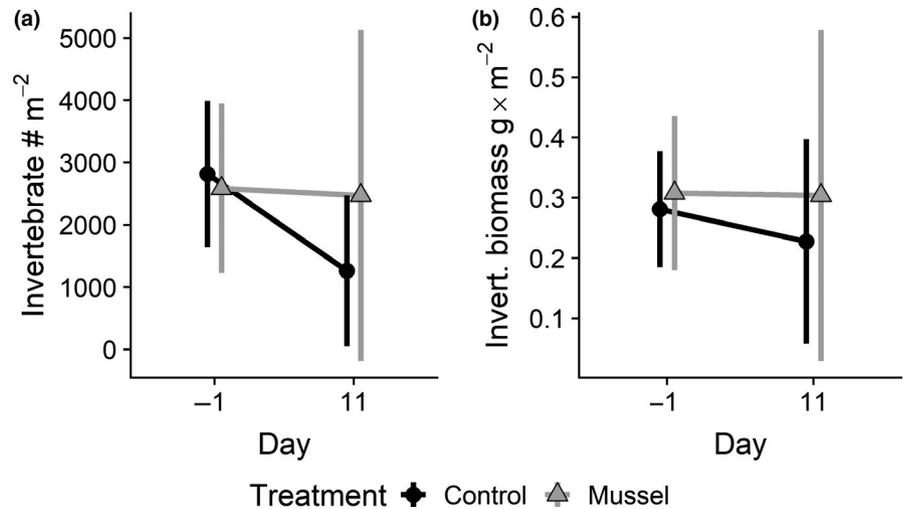
weight change was not significantly different between treatments ($F_{1,16} = 1.38, p = .26$). We then used Cox regression models to investigate whether mesocosm treatment or infection status altered fish survival. Residing in a mussel mesocosm increased survival in fish ($\beta = -.34$, hazard ratio = 0.71, $p = .03$). The median survival (where 50% of the fish are alive) in control mesocosms was 4 days while median survival was 6 days in mussel mesocosms (Figure 3a). Infected fish lived slightly longer than not-infected fish but this relationship was not statistically significant ($\beta = -.07$, hazard ratio = 0.92, $p = .64$). The low β values and high hazard ratio indicate that there was little difference between infected and not-infected fish survival. While fish that resided in mesocosms with mussel assemblages lived longer than fish in control mesocosms, a fish's infection status did not impact survival (Figure 3).

4 | DISCUSSION

We found the fish survived longer in the presence of adult mussels, regardless of their infection status. Our results provide evidence that it is better for fish in a drying system to be in pools with freshwater mussels than in pools without freshwater mussels. This experiment also shows that mussels likely subsidise aquatic food webs whose dynamics are impacted by drought.

Our study mimicked naturally drying streams with limited water input, high water temperatures and high densities as organisms are crowded together in shrinking water volumes. Largemouth bass have a critical thermal maxima near 35°C, though 32°C is the USA EPA recommended temperature for juvenile growth (Brungs & Jones, 1977; US EPA, 1988). Our mesocosms approached the critical thermal maxima for bass on days 11 and 12 for approximately 3 hr. Based on USGS water gage data from 1969 to 1980, the Kiamichi, Little and Glover rivers of south-eastern Oklahoma have an average summer temperature of 27.4, 27.9 and 28.9°C respectively (USGS, 2019). Within these years, maximum water temperatures recorded in these rivers for each year varied from 23 to 35°C. Hopper et al. (2018) observed temperatures from 29.7 to 32.4°C in the Glover River in 2016. Temperatures of 40°C and diel temperature swings of 8°C are not uncommon within Oklahoma rivers (Farless & Brewer, 2017; Matthews & Zimmerman, 1990). While our mesocosms represented the upper limits of what a natural system would experience,

FIGURE 1 Benthic macroinvertebrate density in # m⁻² (a) and dry weight biomass in g/m² (b) for mesocosms with mussels (grey triangles) and without mussels (black circles) at the beginning and end of the experiment. Lines depict the standard deviation while the point represents the mean



these conditions are likely to become more common with climate change (Kaushal et al., 2010). Annual mean air temperatures are expected to rise 4°C in the southern Great Plains for 2041–2070, with the associated summer heatwaves expected to be 0.6° warmer than current heatwaves (Kunkel et al., 2013; Teng, Branstator, Meehl, & Washington, 2016). As water temperatures rise with climate change, stream fish in drying pools will become stressed as the water temperature approaches their critical thermal maxima (Matthews & Zimmerman, 1990). These high water temperatures would also stress the freshwater mussel populations: causing glochidial-brood failure within female mussels and potentially causing glochidia encysted on fish to mature more quickly and at a smaller size (Dudgeon & Morton, 1984; Spooner & Vaughn, 2008). Finally, these increased temperatures could also affect the glochidia–host relationship. While we did not find a difference in survival between infected and not-infected fish, recent research suggests that glochidia can alter the thermoregulation and movement behaviour of its host fish (Horký, Slavík, & Douda, 2019). Thus, projected water temperature increases will threaten freshwater mussels and fishes within pools in intermittent streams.

There were some limitations to our ability to replicate drying pools using mesocosms. Early in the experiment—even before adding fish—oxygen levels in the mesocosms fell to low levels at night due to low-water volume and high algal concentrations. Thus, we supplemented oxygen by aerating the streams to prevent hypoxia and premature fish death. In natural streams, hypoxia would occur at night. However, during drought, dissolved oxygen in drying pools is influenced by the interacting factors of water temperature, primary production, reaeration and depth of the refugia pool (Mosley, 2015). As both temperature and primary production increased during our experiment, dissolved oxygen saturation would steadily decrease each night during our experiment. Thus, we likely recreated the thermal and oxygen regimes of shallow pool refugia with our experimental mesocosms.

While we recreated the abiotic conditions for droughts within our mesocosm, the timing of our experiment is representative of only periodic or seasonal droughts. Seasonal droughts are press

disturbances and the biotic communities that experience seasonal droughts are typically resistant to drought effects and resilient after the predictable return to “normal” conditions (Lake, 2003). Our experiment tested the resistance of largemouth bass to a short seasonal drought. As the fish only survived approximately half of the expected infection period, we do not believe we have enough evidence to state whether infection did or did not affect survival. So, while we do not have enough information to conclude that mussels and fish are conditionally mutualistic, our experiment does provide evidence that adult mussels can increase the survival of largemouth bass during seasonal droughts, likely through the provision of prey items to this invertivorous fish.

We suspect that prey supplemented by adult freshwater mussels, specifically benthic macroinvertebrates, lengthened the fish's survival time. Our control treatments had early fish mortality which would reduce predation pressure on invertebrates and thus allow remaining invertebrates to grow to a larger size and reproduce more by the end of the experiment. Mussel treatments had more fish survive longer; this continual feeding from the macroinvertebrate pool should have reduced the abundance and biomass of that compartment. Without the regeneration of nutrients from mussels, we would expect mussel treatments to have less invertebrates than control treatments based on the length of time fish resided in the mesocosms. Our results suggest otherwise: mussel mesocosms had stable invertebrate abundance and biomass while control mesocosms lost invertebrate abundance and biomass. Our experiment limited terrestrial invertebrate inputs, which are a supplemental prey item for juvenile largemouth bass (Hodgson & Hansen, 2005). This forced the fish to eat benthic invertebrate prey, which have been shown to be increased by the nutrients and habitat provided by mussels (Vaughn & Spooner, 2006). As fish are subjected to increased predation from terrestrial predators during drought (Power, 1984), feeding from the benthos instead of the surface might prevent predation. A study in a southern intermittent stream found that fishes decreased the abundance of benthic macroinvertebrates during intermittency (Wesner, 2013). Because prey were concentrated in the benthos, oxygen was not limiting, and the benthos would represent a thermal refuge, the

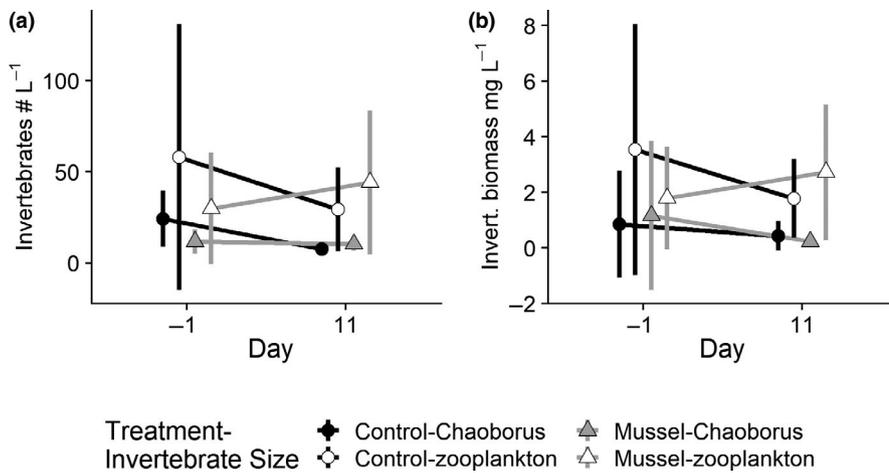


FIGURE 2 Water column invertebrate density in # L⁻¹ (a) and dry weight biomass in mg/m² (b) for mesocosms with (triangle) and without mussels (circle) at the beginning and end of the experiment. We separated larger taxa (Diptera, Coleoptera; filled symbols) and zooplankton (Cladocera, Cyclopoida and small Annelida; white symbols) to illuminate differences in prey quality for the bass. Lines depict the standard deviation while the point represents the mean

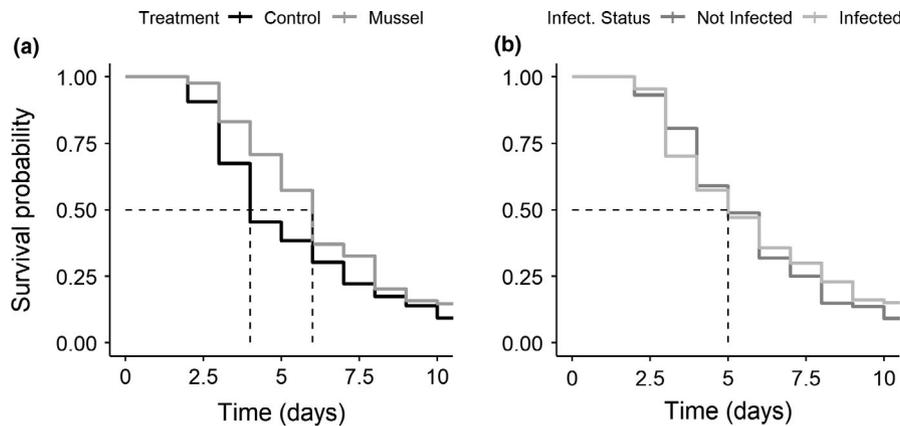


FIGURE 3 Survival curves of fish based on mesocosm treatment (a) and glochidial infection (b). Median survival indicated with the black dashed line. Fish in mussel mesocosms (grey line) had a median survival of 6 days while fish in control mesocosms (black line) had a median survival of 4 days ($\beta = -.34$, hazard ratio = 0.71, $p = .025$). Fish survival was not significantly related to glochidial infection ($\beta = -.07$, hazard ratio = 0.92, $p = .64$). Graph made with code from the R package *survminer* (Kassambara & Kosinski, 2018)

largemouth bass should preferentially feed there (French & Wahl, 2018). After we introduced the invertivorous bass, benthic macroinvertebrate abundance did not increase in the mussel mesocosms, while zooplankton abundance did increase. This potentially describes mesopredator suppression as predatory macroinvertebrates are reduced by the bass and zooplankton increased in abundance (Ritchie & Johnson, 2009; Vance-Chalcraft, Rosenheim, Vonesh, Osenberg, & Sih, 2007). The shift in benthic macroinvertebrate size in control mesocosms, but not mussel mesocosms, is also indicative of intricate food web cascades due to the presence of freshwater mussels and fish; because fish did not survive as long in control tanks, benthic macroinvertebrates in control tanks could grow to larger sizes before consumption. Drought might even be beneficial to bass; Driver and Hoeninghaus (2016) found that concentration in pools leads to larger growth of both juvenile and adult bass. The entangled nature of species-specific tolerance, prey preference and drought makes investigating trophic facilitation in intermittent streams an interesting and unexplored topic.

Streams provide essential ecosystem services to humans (Green et al., 2015), contain unique communities (Dudgeon et al., 2006) and

are increasingly threatened through climate change and anthropogenic water withdrawal (Vorosmarty, Green, Salisbury, & Lammers, 2000; Vorosmarty et al., 2010). Fishes are a dominant part of stream communities and provide many ecosystem services (Holmlund & Hammer, 1999). Fishes are important regulators of aquatic food webs through their consumption of primary producers, macroinvertebrates and other fish (Power, 1990). They provide recreation through fishing and subsequent food (Lynch et al., 2016). Mussels provide many ecosystem services as well; their biofiltration and nutrient capacitance are regulatory services that promote ecosystem stability for all aquatic organisms (Vaughn, 2018; Vaughn & Hoellein, 2018). The overlap of fish and mussel assemblages during low-water periods has additive effects on nutrient cycling (Hopper et al., 2018). Thus, the paired conservation of these assemblages is beneficial to stream ecosystems and the humans that rely on these streams. Droughts are increasing in the Southeastern United States due to climate change (Palmer et al., 2008; Wuebbles, Fahey, & Hibbard, 2017). This poses a challenge for water managers as they struggle to meet urban, agricultural, recreational and ecological needs during climate change-induced water reductions. Maintaining these rivers for the benefit of both recreation and the environmental

needs of endangered species is difficult but can greatly improve the conservation outlook for endangered species (Gates et al., 2015). As recreational fishing contributes to the economy in rural regions (Long & Melstrom, 2016), conserving sport fish is important. We found that fish survival was higher in pools with freshwater mussels than pools lacking freshwater mussels; thus, the conservation of mussels might reduce the drought-induced loss of fishes in rivers. As mussel life history is often connected to fish hosts, their management and conservation should be linked (Modesto et al., 2018). We provide evidence that conservation of freshwater mussels could potentially reduce the loss of more economically viable fishes during anthropogenically exacerbated droughts.

ACKNOWLEDGEMENTS

We dedicate this work to the late Dr. R. Knapp, whose constructive criticism was always kind and thoughtful. Funding was provided by a University of Oklahoma Biological Station fellowship to TPD and NSF DEB-1457542 to CCV. We thank G. Wellborn for guidance conducting the experiment. We appreciate field and laboratory help from M. Carman, N. Ferreira Rodríguez, J. Hartwell, E. Higgins, J. Lopez, R. Prather, B. van Ee and M. Winebarger. We thank E. Marsh-Matthews, M. Patten, M. Busch and the Vaughn laboratory for their advice on the manuscript. Fish were handled in accordance with the recommendations of the American Fisheries Society's Guidelines for the use of Fishes in Research. The protocol was approved by the University of Oklahoma's Institutional Animal Care and Use Committee. This is a contribution to the program of the Oklahoma Biological Survey. The authors of this manuscript have no conflict of interests to report.

AUTHOR CONTRIBUTIONS

TPD and CCV designed the mesocosm experiment, and TPD and KA performed it. TPD performed analyses. All authors wrote the manuscript.

DATA AVAILABILITY STATEMENT

The data sets generated during the current study are available from TPD on reasonable request. Code for analysis is found at <https://github.com/TraciPopejoy/CostlyMutualism>.

ORCID

Traci P. DuBose  <https://orcid.org/0000-0002-9309-4397>

Caryn C. Vaughn  <https://orcid.org/0000-0003-3749-836X>

REFERENCES

ASTM [American Society for Testing and Materials] (2012). *Standard methods for the examination of water and wastewater*. Washington,

- DC: American Public Health Association, American Water Works Association and Water Environment Federation.
- Atkinson, C. L., Julian, J. P., & Vaughn, C. C. (2012). Scale-dependent longitudinal patterns in mussel communities. *Freshwater Biology*, *57*, 2272–2284.
- Atkinson, C. L., & Vaughn, C. C. (2015). Biogeochemical hotspots: Temporal and spatial scaling of the impact of freshwater mussels on ecosystem function. *Freshwater Biology*, *60*, 563–574.
- Atkinson, C. L., Vaughn, C. C., Forshay, K. J., & Cooper, J. T. (2013). Aggregated filter-feeding consumers alter nutrient limitation: Consequences for ecosystem and community dynamics. *Ecology*, *94*, 1359–1369.
- Barnhart, M. C., Haag, W. R., & Roston, W. N. (2008). Adaptations to host infection and larval parasitism in Unionoida. *Journal of the North American Benthological Society*, *27*, 370–394.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software*, *67*, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. *Journal of the North American Benthological Society*, *18*, 308–343.
- Bertrand, K. N., & Gido, K. B. (2007). Effects of the herbivorous minnow, southern redbelly dace (*Phoxinus erythrogaster*), on stream productivity and ecosystem structure. *Oecologia*, *151*, 69–81.
- Bódis, E., Tóth, B., Szekeres, J., Borza, P., & Sousa, R. (2014). Empty native and invasive bivalve shells as benthic habitat modifiers in a large river. *Limnologia*, *49*, 1–9.
- Brungs, W. S., & Jones, B. R. (1977). *Temperature Criteria for Freshwater Fish: Protocols and Procedures*. Duluth, MN: United States Environmental Protection Agency, Office of Research and Development.
- Christensen, E. (1987). Multivariate survival analysis using Cox's regression model. *Hepatology*, *7*, 1346–1358.
- Crane, A. L., Fritts, A. K., Mathis, A., Lisek, J. C., & Barnhart, M. C. (2011). Do gill parasites influence the foraging and antipredator behaviour of rainbow darters, *Etheostoma caeruleum*? *Animal Behaviour*, *82*, 817–823. <https://doi.org/10.1016/j.anbehav.2011.07.015>
- Culp, J. J., Haag, W. R., Arrington, D. A., & Kennedy, T. B. (2011). Seasonal and species-specific patterns in abundance of freshwater mussel glochidia in stream drift. *Journal of the North American Benthological Society*, *30*, 436–445. <https://doi.org/10.1899/10-143.1>
- Dahm, C. N., Baker, M. A., Moore, D. I., & Thibault, J. R. (2003). Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology*, *48*, 1219–1231. <https://doi.org/10.1046/j.1365-2427.2003.01082.x>
- Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: A Challenge for freshwater ecology. *BioScience*, *64*, 229–235. <https://doi.org/10.1093/biosci/bit027>
- Draxler, B., Hove, M. C., Schieffer, S., Berg, M., Widiker, G., Sietman, B., ... Hornbach, D. J. (2006). Suitable host fishes for Fatmucket (*Lampsilis siliquoides*) and Pocketbook (*Lampsilis cardium*) evaluated by high school students and university researchers. *Ellipsaria: Newsletter of Freshwater Mollusk Conservation Society*, *8*, 11–13.
- Driver, L. J., & Hoeinghaus, D. J. (2016). Spatiotemporal dynamics of intermittent stream fish metacommunities in response to prolonged drought and reconnectedness. *Marine and Freshwater Research*, *67*, 1667–1679. <https://doi.org/10.1071/MF15072>
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Leveque, C., ... Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, *81*, 163–182. <https://doi.org/10.1017/S1464793105006950>
- Dudgeon, D., & Morton, B. (1984). Site selection and attachment duration of *Anodonta woodiana* (Bivalvia, Unionacea) glochidia on fish hosts. *Journal of Zoology*, *204*, 355–362.

- Eckblad, J. W. (1971). Weight-length regression models for three aquatic gastropod populations. *The American Midland Naturalist*, *85*, 271–274. <https://doi.org/10.2307/2423940>
- Farless, N. A., & Brewer, S. K. (2017). Thermal tolerances of fishes occupying groundwater and surface-water dominated streams. *Freshwater Science*, *36*, 866–876. <https://doi.org/10.1086/694781>
- Filipsson, K., Petersson, T., Höjesjö, J., Piccolo, J. J., Näslund, J., Wengström, N., & Österling, E. M. (2018). Heavy loads of parasitic freshwater pearl mussel (*Margaritifera margaritifera* L.) larvae impair foraging, activity and dominance performance in juvenile brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, *27*, 70–77.
- French, C. G., & Wahl, D. H. (2018). Influences of dissolved oxygen on juvenile largemouth bass foraging behaviour. *Ecology of Freshwater Fish*, *27*, 559–569. <https://doi.org/10.1111/eff.12370>
- Gagnon, P. M., Golladay, S. W., Michener, W. K., & Freeman, M. C. (2004). Drought responses of freshwater mussels (Unionidae) in coastal plain tributaries of the Flint River basin, Georgia. *Journal of Freshwater Ecology*, *19*, 667–679. <https://doi.org/10.1080/02705060.2004.9664749>
- Gates, K. K., Vaughn, C. C., & Julian, J. P. (2015). Developing environmental flow recommendations for freshwater mussels using the biological traits of species guilds. *Freshwater Biology*, *60*, 620–635. <https://doi.org/10.1111/fwb.12528>
- Giustini, M., Miccoli, F. P., De Luca, G., & Cicolani, B. (2008). Length-weight relationships for some Plecoptera and Ephemeroptera from a carbonate stream in central Apennine (Italy). *Hydrobiologia*, *605*, 183–191. <https://doi.org/10.1007/s10750-008-9353-9>
- Green, P. A., Vörösmarty, C. J., Harrison, I., Farrell, T., Sáenz, L., & Fekete, B. M. (2015). Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change*, *34*, 108–118. <https://doi.org/10.1016/j.gloenvcha.2015.06.007>
- Gutiérrez, J. L., Jones, C. G., Strayer, D. L., & Iribarne, O. O. (2003). Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos*, *101*, 79–90. <https://doi.org/10.1034/j.1600-0706.2003.12322.x>
- Haag, W. R. (2012). *North American freshwater mussels: Natural history, ecology and conservation*. Cambridge, UK: Cambridge U Press.
- Harvey, B. C. (1991). Interactions among stream fishes - Predator-induced habitat shifts and larval survival. *Oecologia*, *87*, 29–36. <https://doi.org/10.1007/BF00323776>
- Hodgson, J. R., & Hansen, E. M. (2005). Terrestrial prey items in the diet of largemouth bass, *Micropterus salmoides*, in a small north temperate lake. *Journal of Freshwater Ecology*, *20*, 793–794.
- Holmlund, C. M., & Hammer, M. (1999). Ecosystem services generated by fish populations. *Ecological Economics*, *29*, 253–268. [https://doi.org/10.1016/S0921-8009\(99\)00015-4](https://doi.org/10.1016/S0921-8009(99)00015-4)
- Hopper, G. W., DuBose, T. P., Gido, K. B., & Vaughn, C. C. (2019). Freshwater mussels alter fish distribution at fine spatial scales through habitat modification. *Freshwater Science*, *38*(4). <https://doi.org/10.1086/705666>
- Hopper, G. W., Gido, K. B., Vaughn, C. C., Parr, T. B., Popejoy, T. G., Atkinson, C. L., & Gates, K. K. (2018). Biomass distribution of fishes and mussels mediates spatial and temporal heterogeneity in nutrient cycling in streams. *Oecologia*, *188*, 1133–1144. <https://doi.org/10.1007/s00442-018-4277-1>
- Horký, P., Slavík, O., & Douda, K. (2019). Altered thermoregulation as a driver of host behaviour in glochidia-parasitised fish. *Journal of Experimental Biology*, *222*, 1–9. <https://doi.org/10.1242/jeb.184903>
- Howerth, E. W., & Keller, A. E. (2006). Experimentally induced glochidiosis in smallmouth bass (*Micropterus dolomieu*). *Veterinary Pathology*, *43*, 1004–1008.
- Johnston, T. A., & Cunjak, R. A. (1999). Dry mass-length relationships for benthic insects: A review with new data from Catamaran Brook, New Brunswick, Canada. *Freshwater Biology*, *41*, 653–674. <https://doi.org/10.1046/j.1365-2427.1999.00400.x>
- Kassambara, A., & Kosinski, M. (2018). *survminer: Drawing Survival Curves using 'ggplot2'*. R package version 0.4.3. Retrieved from <https://CRAN.R-project.org/package=survminer>
- Kaushal, S. S., Likens, G. E., Jaworski, N. A., Pace, M. L., Sides, A. M., Seekell, D., ... Wingate, R. L. (2010). Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment*, *8*, 461–466. <https://doi.org/10.1890/090037>
- Kennedy, T. B., Pugh, S. A., Culp, J. J., & Benke, A. C. (2007). *Quantifying and identifying unionid larvae in drift and on fishes of the Sipse River, Alabama*. Tuscaloosa, AL: Alabama Division of Wildlife and Freshwater Fisheries.
- Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., ... Dobson, J. G. (2013). *Regional Climate Trends and Scenarios for the U.S. National Climate Assessment: Part 4. Climate of the U.S. Great Plains*. NOAA Technical Report NESDIS 142-4 (p. 91). Washington, DC: National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). *ImerTest* package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, *48*, 1161–1172. <https://doi.org/10.1046/j.1365-2427.2003.01086.x>
- Lennox, R. J., Crook, D. A., Moyle, P. B., Struthers, D. P., & Cooke, S. J. (2019). Toward a better understanding of freshwater fish responses to an increasingly drought-stricken world. *Reviews in Fish Biology and Fisheries*, *29*, 71–92. <https://doi.org/10.1007/s11160-018-09545-9>
- Limm, M. P., & Power, M. E. (2011). Effect of the western pearlshell mussel *Margaritifera falcata* on Pacific lamprey *Lampetra tridentata* and ecosystem processes. *Oikos*, *120*, 1076–1082. <https://doi.org/10.1111/j.1600-0706.2010.18903.x>
- Lind, O. T. (1979). *Handbook of common methods in limnology*. St. Louis, MO: Mosby.
- Long, J. M., & Melstrom, R. T. (2016). Measuring the relationship between sportfishing trip expenditures and anglers' species preferences. *North American Journal of Fisheries Management*, *36*, 731–737. <https://doi.org/10.1080/02755947.2016.1167142>
- Lynch, A. J., Cooke, S. J., Deines, A. M., Bower, S. D., Bunnell, D. B., Cowx, I. G., ... Beard, T. D. (2016). The social, economic, and environmental importance of inland fish and fisheries. *Environmental Reviews*, *24*, 115–121. <https://doi.org/10.1139/er-2015-0064>
- Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, *19*, 94–100. <https://doi.org/10.1016/j.tree.2003.10.002>
- Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology*, *48*, 1186–1198. <https://doi.org/10.1046/j.1365-2427.2003.01089.x>
- Matthews, W. J., & Marsh-Matthews, E. (2003). Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology*, *48*, 1232–1253. <https://doi.org/10.1046/j.1365-2427.2003.01087.x>
- Matthews, W. J., & Zimmerman, E. G. (1990). Potential effects of global warming on native fishes of the southern great-plains and the southwest. *Fisheries*, *15*, 26–32. [https://doi.org/10.1577/1548-8446\(1990\)015<0026:PEOGWO>2.0.CO;2](https://doi.org/10.1577/1548-8446(1990)015<0026:PEOGWO>2.0.CO;2)
- Mellilo, J., Richmond, T., & Yohe, G. (2013). *Third National Climate Assessment. National Climate Assessment and Development Advisory Committee*. Washington, DC: NOAA.
- Miserendino, M. L. (2001). Length-mass relationships for macroinvertebrates in freshwater environments of Patagonia (Argentina). *Ecología Austral*, *11*, 3–8.
- Modesto, V., Ilarri, M., Souza, A. T., Lopes-Lima, M., Douda, K., Clavero, M., & Sousa, R. (2018). Fish and mussels: Importance of fish for

- freshwater mussel conservation. *Fish and Fisheries*, 19, 244–259. <https://doi.org/10.1111/faf.12252>
- Mosley, L. M. (2015). Drought impacts on the water quality of freshwater systems; review and integration. *Earth-Science Reviews*, 140, 203–214. <https://doi.org/10.1016/j.earscirev.2014.11.010>
- Naumann, G., Alfieri, L., Wyser, K., Mentaschi, L., Betts, R. A., Carrao, H., ... Feyen, L. (2018). Global changes in drought conditions under different levels of warming. *Geophysical Research Letters*, 45, 3285–3296. <https://doi.org/10.1002/2017GL076521>
- Obaza, A., & Ruehl, C. B. (2013). Regressions for estimating gastropod biomass with multiple shell metrics. *Malacologia*, 56, 343–349. <https://doi.org/10.4002/040.056.0224>
- Palmer, M. A., Liermann, C. A. R., Nilsson, C., Florke, M., Alcamo, J., Lake, P. S., & Bond, N. (2008). Climate change and the world's river basins: Anticipating management options. *Frontiers in Ecology and the Environment*, 6, 81–89. <https://doi.org/10.1890/060148>
- Patterson, M. A., Mair, R. A., Eckert, N. L., Gatenby, C. M., Brady, T., Jones, J. W., ... Devers, J. L. (2018). *Freshwater Mussel Propagation for Restoration*. New York, NY: Cambridge University Press.
- Pires, D. F., Pires, A. M., Collares-Pereira, M. J., & Magalhaes, M. F. (2010). Variation in fish assemblages across dry-season pools in a Mediterranean stream: Effects of pool morphology, physicochemical factors and spatial context. *Ecology of Freshwater Fish*, 19, 74–86. <https://doi.org/10.1111/j.1600-0633.2009.00391.x>
- Power, M. E. (1984). Depth distributions of armored catfish: Predator-induced resource avoidance? *Ecology*, 65, 523–528. <https://doi.org/10.2307/1941414>
- Power, M. E. (1990). Effects of fish in river food webs. *Science*, 250, 811–814.
- R Core Team, (2019). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. R version 3.5.3.
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998.
- Rogers, C. L., & Dimock, R. V. (2003). Acquired resistance of bluegill sunfish *Lepomis macrochirus* to glochidia larvae of the freshwater mussel *Utterbackia imbecillis* (Bivalvia: Unionidae) after multiple infections. *Journal of Parasitology*, 89, 51–57.
- Sansom, B. J., Atkinson, J. F., & Bennett, S. J. (2017). Modulation of near-bed hydrodynamics by freshwater mussels in an experimental channel. *Hydrobiologia*, 810, 449–463.
- Sansom, B. J., Bennett, S. J., Atkinson, J. F., & Vaughn, C. C. (2018). Long-term persistence of freshwater mussel beds in labile river channels. *Freshwater Biology*, 63, 1469–1481.
- Schlosser, I. J. (1987). The role of predation in age-related and size-related habitat use by stream fishes. *Ecology*, 68, 651–659.
- Spooner, D. E., & Vaughn, C. C. (2006). Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology*, 51, 1016–1024.
- Spooner, D. E., & Vaughn, C. C. (2008). A trait-based approach to species' roles in stream ecosystems: Climate change, community structure, and material cycling. *Oecologia*, 158, 307–317.
- Stachowicz, J. J. (2001). Mutualism, facilitation, and the structure of ecological communities. *BioScience*, 51, 235–246.
- Stoffels, R. J., Karbe, S., & Paterson, R. A. (2003). Length-mass models for some common New Zealand littoral-benthic macroinvertebrates, with a note on within-taxon variability in parameter values among published models. *New Zealand Journal of Marine and Freshwater Research*, 37, 449–460.
- Strayer, D. L. (1999). Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society*, 18, 468–476.
- Strayer, D. L. (2014). Understanding how nutrient cycles and freshwater mussels (Unionoida) affect one another. *Hydrobiologia*, 735, 277–292.
- Teng, H. Y., Branstator, G., Meehl, G. A., & Washington, W. M. (2016). Projected intensification of subseasonal temperature variability and heat waves in the Great Plains. *Geophysical Research Letters*, 43, 2165–2173.
- Therneau, T. M. (2015). *A package for survival analysis in S. R Package Version 2.38*. Retrieved from <https://CRAN.R-project.org/package=survival>
- Therneau, T. M., & Grambsch, P. M. (2000). *Modeling survival data: Extending the Cox Model*. New York, NY: Springer Science+Business Media.
- Thomas, G. R., Taylor, J., & Garcia de Leaniz, C. (2013). Does the parasitic freshwater pearl mussel *M. margaritifera* harm its host? *Hydrobiologia*, 735, 191–201.
- US EPA [United States Environmental Protection Agency] (1988). *Temperature: Water quality standards criteria summaries: A Compilation of State/Federal Criteria*. Washington, DC: US Environmental Protection Agency, Office of Water Regulations and Standards.
- Wuebbles, D. J., Fahey, D. W., & Hibbard, K. A. (Eds.). (2017). *Climate science special report: fourth national climate assessment*. Vol. I, (470pp), Washington, DC: U.S. Global Change Research Program. <https://doi.org/10.7930/JOJ964J6>
- USGS [United States Geologic Survey]. (2019). *National Water Information System*. data available on the World Wide Web (USGS Water Data for the Nation). Retrieved from: <https://nwis.waterdata.usgs.gov/nwis/qwdata>
- Vance-Chalcraft, H. D., Rosenheim, J. A., Vonesh, J. R., Osenberg, C. W., & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: A meta-analysis. *Ecology*, 88, 2689–2696.
- Vaughn, C. C. (2018). Ecosystem services provided by freshwater mussels. *Hydrobiologia*, 810, 15–27.
- Vaughn, C. C., & Hoellein, T. J. (2018). Bivalve impacts in freshwater and marine ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 49, 183–208.
- Vaughn, C. C., Nichols, S. J., & Spooner, D. E. (2008). Community and foodweb ecology of freshwater mussels. *Journal of the North American Benthological Society*, 27, 409–423.
- Vaughn, C. C., & Spooner, D. E. (2006). Unionid mussels influence macroinvertebrate assemblage structure in streams. *Journal of the North American Benthological Society*, 25, 691–700.
- Vaughn, C. C., Spooner, D. E., & Galbraith, H. S. (2007). Context-dependent species identity effects within a functional group of filter-feeding bivalves. *Ecology*, 88, 1654–1662.
- Vaughn, C. C., & Taylor, C. M. (2000). Macroecology of a host-parasite relationship. *Ecography*, 23, 11–20.
- Vorosmarty, C. J., Green, P., Salisburry, J., & Lammers, R. B. (2000). Global water resources: Vulnerability from climate change and population growth. *Science*, 289, 284–288.
- Vorosmarty, C. J., McIntyre, P. B., Gessnerboli, M. O., Dudgeon, D., Prusevich, A., Green, P., ... Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555–561. <https://doi.org/10.1038/nature09440>
- Weins, J. A. (1977). On competition and variable environments: Populations may experience "ecological crunches" in variable climates, nullifying the assumptions of competition theory and limiting the usefulness of short-term studies of population patterns. *American Scientist*, 65, 590–597.
- Wesner, J. S. (2013). Fish predation alters benthic, but not emerging, insects across whole pools of an intermittent stream. *Freshwater Science*, 32, 438–449. <https://doi.org/10.1899/12-124.1>
- Whitney, J. E., Al-Chokhachy, R., Bunnell, D. B., Caldwell, C. A., Cooke, S. J., Eliason, E. J., ... Paukert, C. P. (2016). Physiological basis of climate change impacts on North American Inland fishes. *Fisheries*, 41, 332–345. <https://doi.org/10.1080/03632415.2016.1186656>
- Williams, J. D., Bogan, A. E., Butler, R. S., Cummings, K. S., Garner, J. T., Harris, J. L., ... Watters, G. T. (2017). A Revised list of the freshwater

- mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. *Freshwater Mollusk Biology and Conservation*, 20, 33–58. <https://doi.org/10.31931/fmbc.v20i2.2017.33-58>
- Wolff, P. J., Taylor, C. A., Heske, E. J., & Schooley, R. L. (2016). Predation risk for crayfish differs between drought and nondrought conditions. *Freshwater Science*, 35, 91–102. <https://doi.org/10.1086/683333>
- Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365, 2093–2106. <https://doi.org/10.1098/rstb.2010.0055>

How to cite this article: DuBose TP, Ashford K, Vaughn CC. Freshwater mussels increase survival of largemouth bass (*Micropterus salmoides*) in drying pools. *Ecol Freshw Fish*. 2019;00:1–10. <https://doi.org/10.1111/eff.12508>