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REPORT

A Tale of Two Rivers: Implications of Water Management Practices for Mussel Biodiversity Outcomes During Droughts

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Abstract Droughts often pose situations where stream water levels are lowest while human demand for water is highest. Here we present results of an observational study documenting changes in freshwater mussel communities in two southern US rivers during a multi-year drought. During a 13-year period water releases into the Kiamichi River from an impoundment were halted during droughts, while minimum releases from an impoundment were maintained in the Little River. The Kiamichi observed nearly twice as many low-flow events known to cause mussel mortality than the Little, and regression tree analyses suggest that this difference was influenced by reduced releases. During this period mussel communities in the Kiamichi declined in species richness and abundance, changes that were not observed in the Little. These results suggest that reduced releases during droughts likely led to mussel declines in one river, while maintaining reservoir releases may have sustained mussel populations in another.

Keywords Drought · Minimum flows · Hydrologic alteration · Environmental flows · Unionoida · Freshwater mussel · Indicator species

INTRODUCTION

Water sustainability is a widespread issue in North America and across the globe as humans are using freshwater more rapidly than it can be replenished (Baron et al. 2002; Richter et al. 2003). In the United States, sustainable water use is not only a concern in the arid southwest (Sabo et al. 2010) but even in humid areas such as the southeast (Pederson et al. 2012). Freshwater is vital for human life, but biologically complex and intact freshwater ecosystems provide key ecosystem services that also benefit society

(Baron et al. 2002). With increasing human water demand coupled with climate change induced alterations of drought frequency (IPCC 2007) and stream flows (Milly et al. 2005), the trade-offs between water security for human needs and environmental conservation will be only more challenging in the future.

Freshwater mussels (Bivalvia: Unionidae, hereafter "mussels") are one of the most imperiled faunas due to species extinctions and declines of once common species (Strayer 2008; Haag 2012). The influence of stream flows on mussels is pervasive, making them a model study system to investigate the environmental effects of hydrological alterations. Mussels rely on predictable stream flows for reproduction (Galbraith and Vaughn 2011), the maintenance of tolerable temperatures (Gagnon et al. 2004; Spooner and Vaughn 2008; Gough et al. 2012) and stable habitats (Allen and Vaughn 2010), as well as the abundance of host fish required for juvenile mussel recruitment (Roy et al. 2005; Vaughn 2012). Changes in hydrology due to dam construction and river channelization is considered to be the primary cause of mussel declines in the US (Vaughn and Taylor 1999; Strayer et al. 2004), and effects of climate change and water withdrawals are predicted to accelerate mussel declines in the future (Spooner et al. 2011).

Mussels are patchily distributed in streams, and typically occur in multi-species, aggregated assemblages known as "mussel beds." Mussel species within these beds vary in behavior and physiology, including thermal tolerance (Vaughn 2010). Spooner and Vaughn (2008) investigated the effects of naturally occurring temperatures (5–35 °C) on the physiological condition of eight common mussel species in the southern US, and found that species are either thermally sensitive or tolerant based on their response to warm temperatures (35 °C). While all mussel

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species are susceptible to mortality and stranding during droughts, thermally sensitive species are more likely to perish during high temperature and low-flow conditions (Galbraith et al. 2010).

Here we present results of an observational study examining water management practices and changes in mussel communities in two rivers during a multi-year drought. The Kiamichi and Little Rivers, located in the southern plains of the US, are similar in size and mussel species composition but were managed differently during a recent, multi-year drought (1998–2005; Galbraith et al. 2010): in the Kiamichi River water releases into the river from a tributary impoundment decreased as the drought progressed, while in the Little River water releases into the river were maintained during the drought. We use long-term data from each river to compare mussel species richness and community structure before and after the drought and discuss how these results likely relate to water management practices.

MATERIALS AND METHODS

Study Area

We collected pre (1991–1994) and post (2003–2006) drought mussel data from two adjacent rivers in south-eastern Oklahoma, US, the Kiamichi and Little Rivers (Fig. 1). Table 1 summarizes the mussel species in these rivers presently and historically. Mussel data from Isely (1924) were collected in 1910–1911 prior to dam construction on these rivers, though only a few sites were sampled: 3 in the Kiamichi and 1 in the Little. Present-day sampling efforts have been much more extensive, as we present data from 7 sites in the Kiamichi River (Galbraith et al. 2010) and 8 sites in the Little River. In total, 35 mussel species have been reported in these rivers, 31 from the Kiamichi River, and 33 from the Little River with 29 species common to both rivers (Table 1). Therefore, the mussel communities in these rivers, while not identical, are
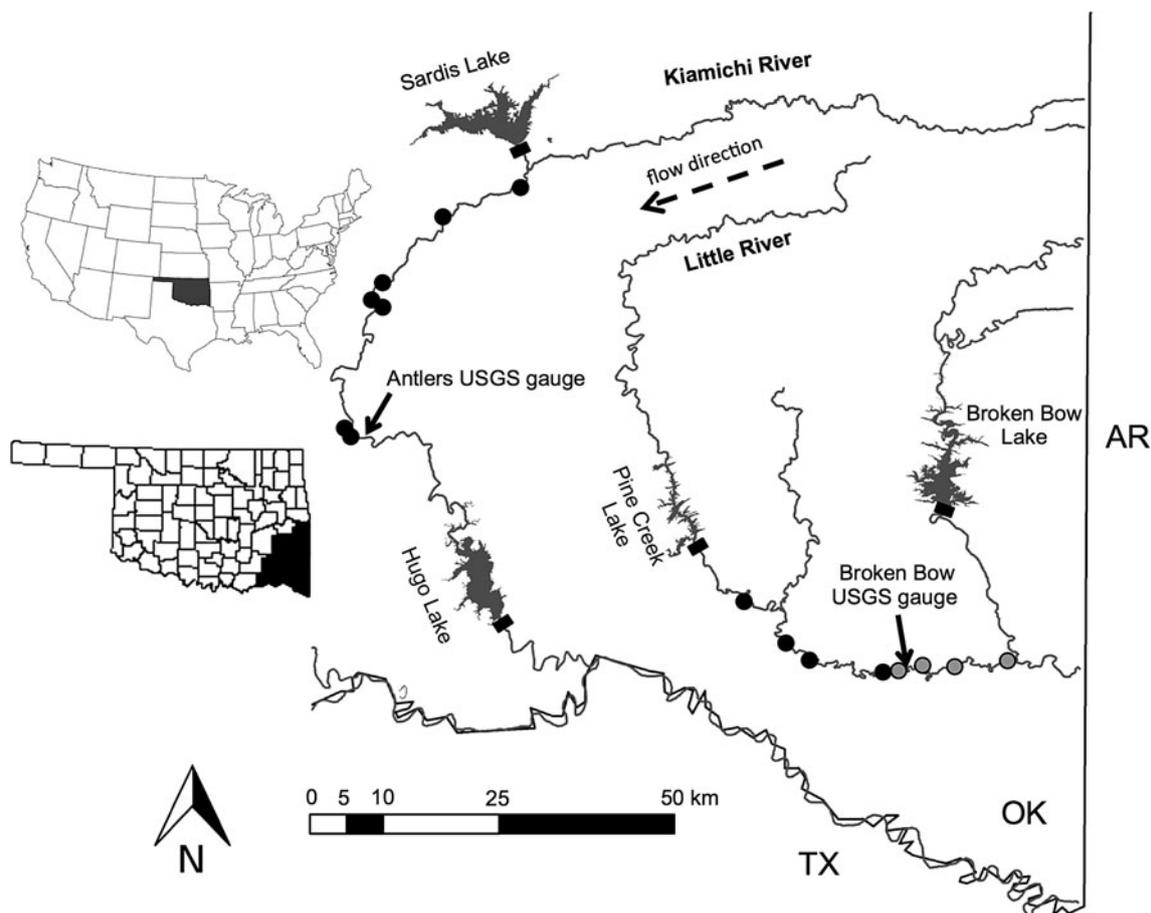
Fig. 1 Map of Little and Kiamichi River drainages in southeastern Oklahoma (OK), bordering Arkansas (AR) and Texas (TX). *Black rectangles* represent dams, *circles* represent mussel sampling sites, and *arrows* point to USGS stream gauges. Kiamichi River sampling sites and mussel data are presented in Galbraith et al. (2010). On the Little River, *black circles* represent sites with only timed search data, while *gray circles* represent sites with both timed search and quadrat data

strikingly similar. Both rivers originate in the Ouachita Uplands then flow south through the Gulf Coastal Plain and are known for their high aquatic biodiversity (Matthews et al. 2005; Galbraith et al. 2008). The climate in this region is characterized by cyclical droughts (Matthews et al. 2005) and rivers here are considered especially vulnerable to climate warming (Mulholland et al. 1997; Matthews et al. 2005).

Rivers in southeast Oklahoma are targeted by nearby metropolitan areas (Oklahoma City, OK, and Dallas-Fort Worth, TX) as water sources to meet future water needs (OWRB 2012). Stream flows at our sampling sites on the Little River are affected by releases from a mainstem impoundment, Pine Creek Lake, while stream flows at the Kiamichi River sampling sites are affected by a tributary impoundment, Sardis Lake, which impounds Jackfork Creek (~30 % of the Kiamichi River watershed). However, water management practices of these two reservoirs differ. Releases from Sardis Lake (Kiamichi River) are managed to maintain lake levels for human consumption and recreation, so no water is released during droughts. Although releases from Pine Creek Lake (Little River) vary throughout the year to maintain lake levels and prevent floods, they are maintained at a minimum of at least $0.51 \text{ m}^3 \text{ s}^{-1}$ as a "water quality release" to dilute effluent from a paper mill downstream in Valliant, OK (Dave Martinez, United States Fish and Wildlife Service, personal communication).

Mussel Sampling

Long-term mussel monitoring sites were established on the Kiamichi River in 1991 by Vaughn and Pyron (1995). These sites were resampled in 2003–2005 at the end of the drought, and Galbraith et al. (2010) documented declines in both mussel species richness and abundance. Sampling methods for the Kiamichi River are described in detail in Galbraith et al. (2010), but consisted of excavating 15 quadrats per site at each time period during the summer. The Little River was surveyed for mussels in the summer of 1992–1994 (Vaughn and Taylor 1999), and we resurveyed 8 of the same sites during the summer of 2005–2006. The selected sites were located between Pine Creek Lake and the confluence with the Mountain Fork River (Fig. 1), since mussel beds in this stretch of the river were found to have the highest mussel abundances and species richness (Vaughn and Taylor 1999).

For both sampling periods in the Little River, mussels were sampled semi-quantitatively (timed searches) at all 8 sites, and quantitatively sampled (0.25 m^2 quadrat excavation) at 4 of these sites (Fig. 1). Timed searches varied in total duration among sites and years but were always between 1 and 2 h. From these samples, we calculated

mussel species richness and abundance (mean density from quadrats and catch-per-unit-effort from timed searches). The number of excavated quadrats was 15 for all sites in the 1990s, but in the 2000s we sampled 24 quadrats for

Table 1 Mussel species collected from Kiamichi and Little Rivers. Data from 1910 to 1911 was collected by Isely (1924) from 3 sites on the Kiamichi and 1 site on the Little before the construction of the Sardis and Pine Creek dams. Data from the Kiamichi River collected in 2003–2005 is presented in Galbraith et al. (2010), and data from the Little River collected in 2006 is presented in this paper

Species	Kiamichi River		Little River	
	1910–1911	2003–2005	1910–1911	2006
Actinonaias ligamentina	X	X	X	X
Amblema plicata	X	X	X	X
Arkansia wheeleri	X	X		X
Ellipsaria lineolata	X	X	X	X
Elliptio dilatata	X			X
Fusconaia flava	X	X		X
Lampsilis cardium	X	X		X
Lampsilis siliquoidea	X	X	X	X
Lampsilis teres	X	X	X	X
Lasmigona costata		X		X
Leptodea leptodon	X	X		
Leptodea fragilis	X	X		X
Megalonaias nervosa	X	X		X
Obliquaria reflexa	X	X	X	X
Obovaria jacksonia	X	X	X	X
Pleurobema rubrum	X		X	X
Pleurobema sintoxia	X	X		X
Plectomerus dombeyanus			X	X
Potamilus purpuratus	X	X	X	X
Potamilus capax	X			
Ptychobranchus occidentalis	X	X		X
Pyganadon grandis	X	X		X
Quadrula cylindrica		X	X	X
Quadrula fragosa			X	X
Quadrula quadrula	X	X	X	X
Quadrula pustulosa	X	X	X	X
Quadrula verrucosa	X	X	X	X
Strophitus undulatus	X	X		X
Truncilla donaciformis	X		X	X
Truncilla truncata	X	X	X	X
Toxolasma parvus	X	X		X
Toxolasma texasensis				X
Utterbackia imbecillis	X	X		X
Villosa arkansasensis				X
Villosa leinosa	X			X
Total	29	26	17	32

three of the four sites, and 15 for the fourth. Variation in sampling effort (number of quadrats or time searched) between sites or sampling periods has the potential to affect species-richness data of each site, as increased sampling increases the chances of collecting a rare or uncommon species. To correct for effects of varied sampling effort on species richness data, we generated rarefaction curves using EcoSim (version 7.72; Acquired Intelligence, Inc.). To calculate rarefied species richness for the three sites with 24 quadrats, we simulated 1000 resamples to generate a rarefaction curve to estimate species richness for 15 quadrat samples. For timed search data, we calculated rarefied species richness for whichever of the two samples (1990s or 2000s) had the larger total number of mussels collected, simulating 1000 resamples with the number of individuals from the smaller sample. Following Galbraith et al. (2010), we calculated the relative abundance of mussel species contributing to the two thermal guilds based on their response to warm temperatures (35 °C; thermally sensitive: *Actinonaias ligamentina*, *Lampsilis cardium*, *Quadrula pustulosa*, *Truncilla truncata*; thermally tolerant: *Amblema plicata*, *Fusconaia flava*, *Megalonaias nervosa*, *Obliquaria reflexa*; Spooner and Vaughn 2008).

Hydrological and Climate Data

Daily discharge data for the Little River were obtained from USGS gauging station 0733850 near Broken Bow, OK (waterdata.usgs.gov/ok), the closest gauging station to our sampling sites (Fig. 1). Data were obtained from the construction of Pine Creek Lake (1970) through our mussel sampling (2006). Because we wanted to compare our Little River results to those documented in the Kiamichi River (Galbraith et al. 2010), we also obtained daily discharge data from USGS gauging station 07336200 in the Kiamichi River near Antlers (Fig. 1), spanning the construction of Sardis Lake (1982) through the mussel sampling (2005, Galbraith et al. 2010). The Kiamichi River and Little River are similar in size at these two gauges (2947 and 3175 km^2, respectively). We defined a low-flow threshold as the 5th-quantile of discharges (Kiamichi River, 0.08 m^3 s^{-1}; Little River, 0.96 m^3 s^{-1}), following Galbraith et al. (2010). This discharge corresponds to dates where we observed exposed portions of mussel beds, dead stranded mussels, non-flowing river sections, and isolated pools while sampling the Little River in 2005 and 2006. Moreover, an in situ experiment conducted in the Kiamichi River showed high rates of mussel mortality in isolated pools at these discharges (Galbraith et al. 2010). This low-flow threshold simply represents a discharge that is known to cause mussel mortality in these rivers, and is not meant to indicate a minimum flow requirement to sustain freshwater mussels in these rivers (which would require more study).

Data on water flowing into (inflows) and released from Pine Creek Lake (Little River) and Sardis Lake (Kiamichi River) were obtained from the Army Corp of Engineers (www.swt-wc.usace.army.mil/PINEcharts.html and www.swt-wc.usace.army.mil/SARDcharts.html, respectively). Data on inflows and releases were not available before 1995, so we examined data from 1995 through our sampling period (2006). Using these data, we calculated the release/inflow ratio, where a value of one indicates that the reservoir released the same volume of water that flowed into it and a value greater or less than one indicates the reservoir released relatively more or less water than flowed into it, respectively.

We obtained air temperature and precipitation data from the Oklahoma Mesonet (www.mesonet.org), a system of continuous-recording weather stations. Using data from 9 stations across four counties that span the Little River and Kiamichi River watersheds, Galbraith et al. (2010) reported that this region experienced a multi-year drought from 1998 to 2005 when compared to the historical temperature and precipitation record. In our analysis, we used data collected from 4 stations in the Kiamichi River watershed (located in Antlers, Clayton, Hugo, and Talihina) and 4 stations in the Little River watershed (located in Broken Bow, Cloudy, Idabel, and Mt. Herman). We calculated monthly average high air temperatures using daily high air temperature data, and used monthly total precipitation data, which was only available beginning in March of 1997.

Statistical Analyses

To test for changes in mussel communities between the 1990s and 2000s, we used paired *t* tests on mussel data (running separate tests for each river): mussel species richness (rarefied when necessary to account for varying sampling effort), mussel abundance (density for quadrat data [individuals per m^2] and catch-per-unit effort for timed search data [individuals per hour]), and the relative abundance of thermally sensitive species (an additional test for thermally tolerant species was not conducted as it would have been redundant). Abundance data were square root transformed and relative abundance data were arcsine-square root transformed prior to analysis. To test for differences between the frequency of low-flow days between the Kiamichi and Little Rivers, we used Fisher's exact test on a contingency table with the cumulative number of low-flow days and non-low-flow days that occurred between 1994 and 2006. Finally, to investigate how climate and water management influenced the occurrence of low-flow days on the Kiamichi and Little Rivers, we used regression tree models. Regression tree models are non-parametric, distribution-free, robust to outliers, do not require a priori hypotheses, and can model threshold responses and
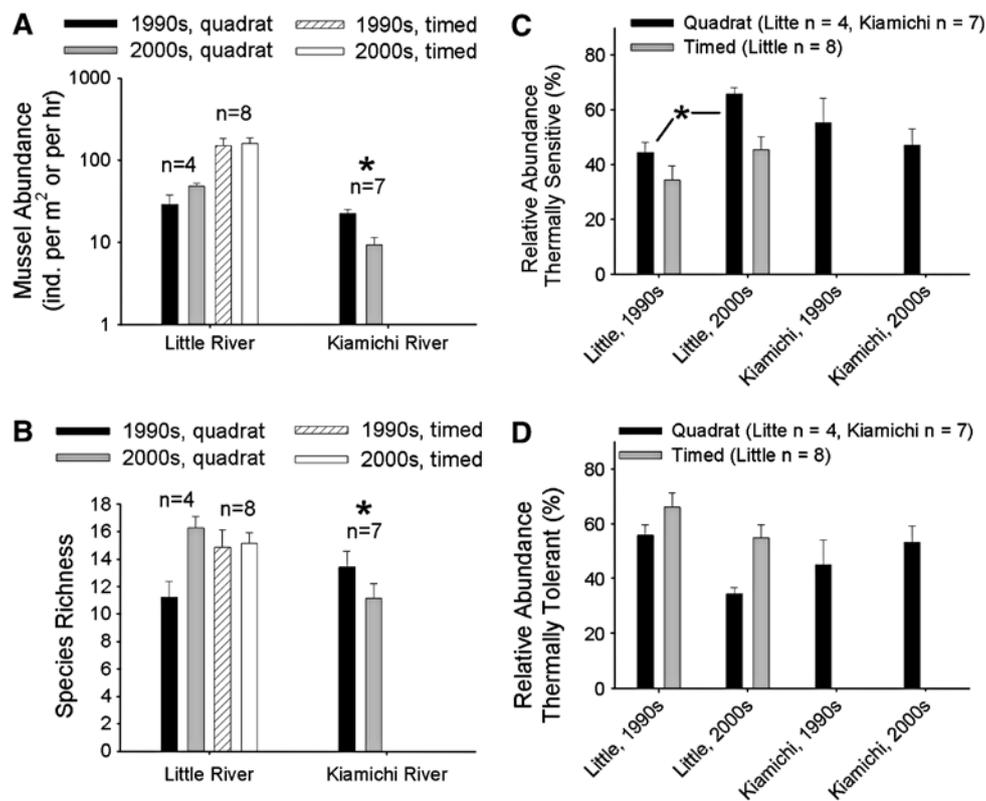
Fig. 2 Summary of mussel community data from Little River sites sampled in 1992–1994 ("1990s") and 2005–2006 ("2000s"), data from Kiamichi River sites sampled in 1990–1992 and 2003–2005 reproduced from Galbraith et al. (2010). **a** Mussel abundance from quadrat (mussels per m²) and timed search samples (mussels collected per hour), *bars* are means and whiskers are SEs; **b** mussel species richness from quadrat and timed search samples, *bars* are means and whiskers are SEs; and **c** relative abundances of thermally tolerant ("tolerant") and thermally sensitive ("sensitive") mussel species from quadrat and timed search samples, *stacked bars* indicate means. See Spooner and Vaughn (2008) for further clarification of thermal guilds. Sample sizes (number of sites) are noted above the *bars*

complex interactions (De'ath and Fabricius 2000). Regression trees model a continuous response variable by repeatedly splitting the data into groups, defined by simple decision rules based on a single explanatory variable. We used monthly data for our regression tree models, with number of low-flow days per month as the response variable (March 1997–December 2006). For candidate explanatory variables we used: average high air temperature (°C), total precipitation in the current month (cm), total precipitation in the previous month (cm), and the release/inflow ratio (described above). We generated regression trees for each river individually to examine differences between the two rivers. Regression trees were generated using the "tree" package for R software (Ver. 2.13.1, R Development Core Team). Categorical and regression tree analyses are generally conducted by growing a very large tree, and then pruning it into a smaller, more parsimonious tree. We selected the smallest tree size within one standard error of the tree with the smallest average estimated error rate from 50 cross-validation runs (1-SE rule, De'ath and Fabricius 2000). This approach

prunes trees by removing branches that do not explain a significant amount of error.

RESULTS

Mussel Data

Mussel communities in the Little River were diverse and abundant during both sampling periods (Fig. 2a, b), and paired *t* tests indicated no significant differences in abundance (quadrat: $t = 1.67$, df = 3, $p = 0.20$; timed: $t = 0.46$, df = 7, $p = 0.66$) or species richness (quadrat: $t = 2.66$, df = 3, $p = 0.08$; timed: $t = 0.40$, df = 7, $p = 0.70$). However, during the same time span in the Kiamichi River mussel abundance and species richness showed significant declines (abundance: $t = -4.60$, df = 6, $p = 0.004$; richness: $t = -3.36$, df = 6, $p = 0.015$; Fig. 2a, b). Mussel communities in these rivers also showed different trends in the composition of thermally sensitive species. Data from the Little River indicate that mussel species more sensitive
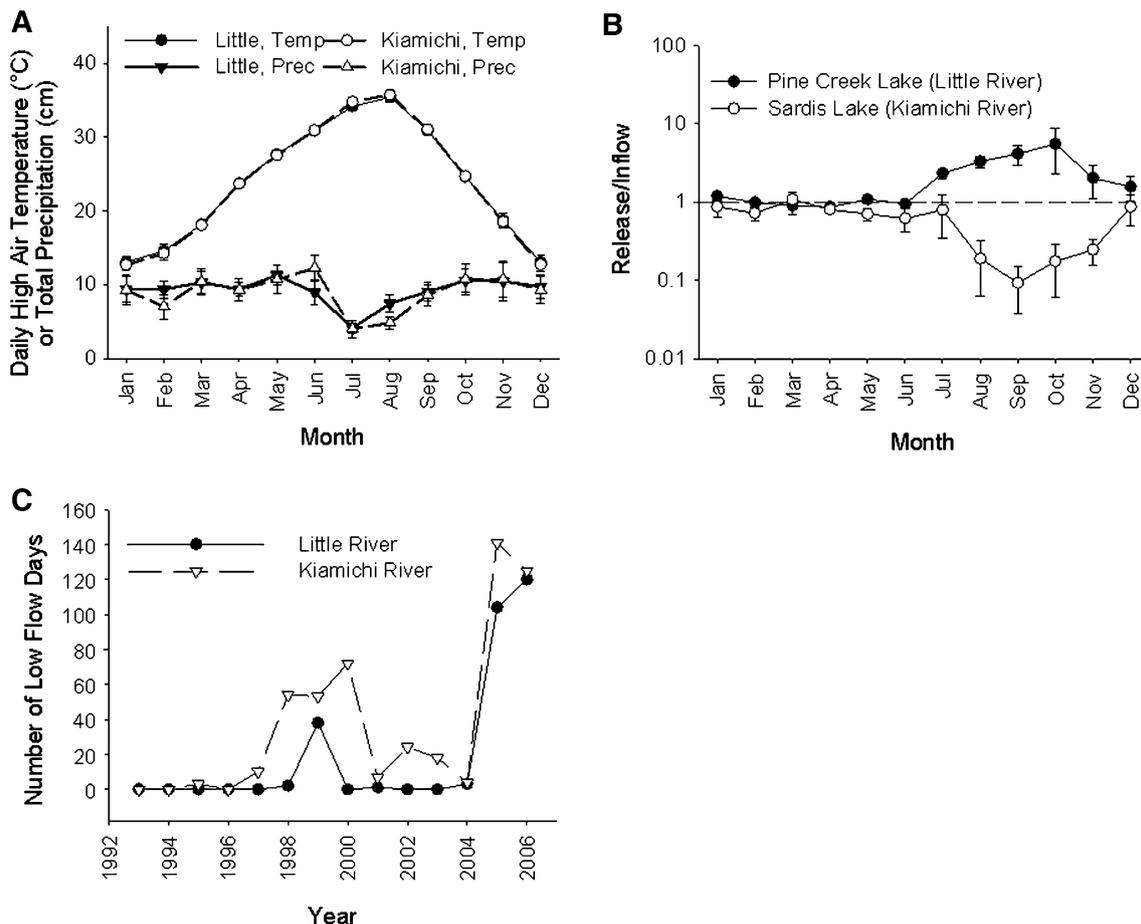
Fig. 3 Summary of climate and hydrological data during the mussel sampling periods for the Little River (1994–2006) and Kiamichi River (1993–2005). **a** Mean daily high air temperature (°C) and total precipitation (cm) by month (data from Oklahoma Mesonet), points are means and whiskers are SEs; **b** release by inflow ratios for reservoirs influencing streamflows at mussel sampling sites on the Little River (Pine Creek Lake) and the Kiamichi River (Sardis Lake) by month (data from US Army Corp of Engineers), points are means and whiskers are SEs (note log-scale on *y*-axis). The *dashed line* indicates a release/inflow ratio of one, indicating equal amounts of water flowing into and released from the lake; **c** total number of low-flow days for the Little and Kiamichi Rivers for each year (using the 5th-quantile of historical post-dam discharges as the low-flow threshold; data from US Geological Survey)

to warm temperatures increased in abundance relative to thermally tolerant species (Fig. 2c, d), but this relationship was only significant for quadrat data and not timed search data (quadrat: $t = 10.93$, df = 3, $p = 0.002$; timed: $t = 1.7006$, df = 7, $p = 0.13$) in spite of the greater sample size of the timed search data ($n = 8$ vs. $n = 4$). Because of this, we refrain from interpreting the results of the significant test on quadrat data when it is insignificant with timed search data, and interpret these tests together as indicating that there was no significant change in the relative abundance of thermally tolerant species in the Little River. In contrast, mussel communities in the Kiamichi River showed the opposite relationship where mussel species more sensitive to warm temperatures decreased in abundance relative to thermally tolerant species, but this trend was not significant ($t = -0.95$, df = 6, $t = 0.38$, Fig. 2c, d).

Climate and Hydrologic Data

Both the Kiamichi River and Little River experienced a similar climate, with the late summer months (July, August, and September) characterized by the hottest and driest times of year (Fig. 3a). However, reservoir water management practices differed between the rivers, especially between July and November (Fig. 3b). In the Little River, Pine Creek Lake maintained a constant release, with a release/inflow ratio always >1 in these months. Over 12 years, less than half of months observed a release/inflow ratio <1 (71 of 144). Release/inflow ratios <1 were typically observed in March and April (10 of 12 years) and in June (9 of 12 years). In fact, the highest release/inflow ratios for Pine Creek Lake coincided with the driest part of the year (July to November, Fig. 3a, b). In the Kiamichi

A Little River (psuedo-R² = 0.45)   **B** Kiamichi River (psuedo-R² = 0.66)

Release/Inflow > 5.5

18.33 (9)   0.95 (109)

Prev. Prec. < 5.5 cm

Release/Inflow < 0.20   0.18 (60)

Prev. Prec. < 1.4 cm   0.80 (20)

25.4 (5)   Prec. < 3.2 cm

23.8 (5)   Avg. Temp > 20.4 °C

10.45 (22)   0.83 (6)
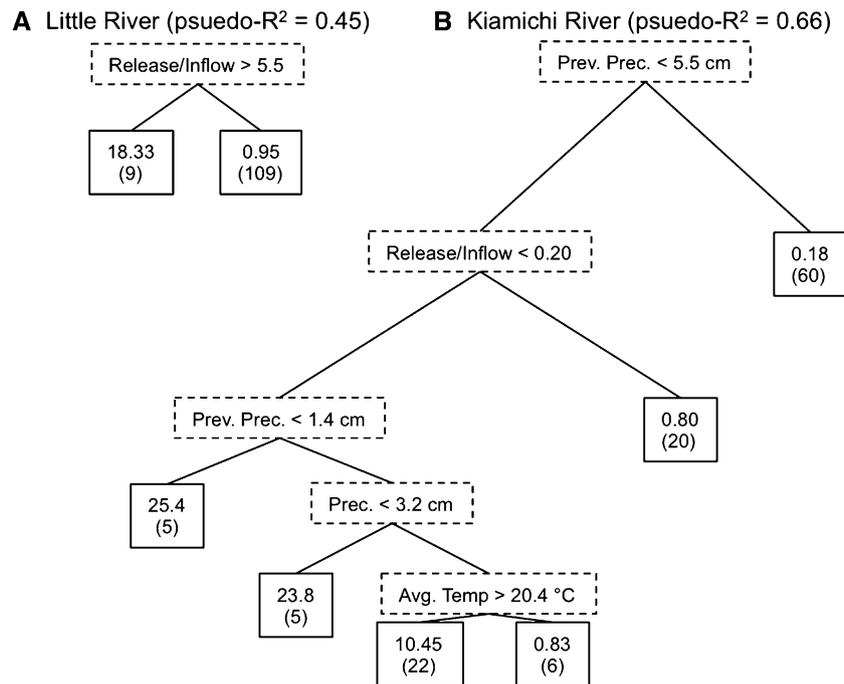
Fig. 4 Regression trees predicting the number of low-flow days in a month for the Little and Kiamichi Rivers (**a** and **b**, respectively). Regression trees are read from top to bottom, with the *top* representing the root of the tree that splits the dataset along the branches of the tree into terminal leaves. Each decision rule (*dashed box*) splits the data into subsets based upon whether the data are greater or less than a given value of the explanatory variable; if the decision rule is true then the data is split along the left-hand branch toward an increase in low-flow days per month. Each terminal leaf (*solid box*) contains a subset of the data, with the mean number of low-flow days in a month shown, and the subset sample size in parentheses. Within a tree, the lengths of the vertical branches indicate the amount of relative error explained each by split. *Prec.* Total monthly precipitation; *Prev. Prec.* total precipitation in previous month; *Avg. Temp.* average daily high air temperature; *release/inflow* release/inflow ratio

River, Sardis Lake typically released much less water than it received via inflow. Over 12 years, 85 % of all months observed a release/inflow ratio <1 (123 of 144). Moreover, 40 % (57 of 144) of all months had no water released from the lake at all. Furthermore, these zero-release months most frequently occurred in the hottest and driest part of the year (August, 10 of 12 years; July and September, 8 of 12 years). Finally, these two rivers also significantly differed in the number of low-flow days observed during the study period (Fisher's exact test, $p < 0.001$, Fig. 3c). From 1994 to 2006 there were nearly twice as many low-flow days in the Kiamichi River compared to the Little River (511 compared to 268), and these low-flow days occurred more frequently in the Kiamichi River than in the Little River (11 of 14 years for the Kiamichi River, and 6 of 14 years for the Little River). Additionally, the number of low-flow days in the Kiamichi River outnumbered those in the Little River in every year they occurred.

Regression tree models were successful in using climate and reservoir management data to explain the occurrence of low-flow days. However, the regression tree models for the Little River and Kiamichi Rivers were strikingly different (Fig. 4). The regression tree model for the Little River explained less error than the Kiamichi River model (pseudo-

R^2 0.45 and 0.66, respectively). Furthermore, the Little River tree model was much simpler than the Kiamichi River tree model, with only a single branching point and two terminal leaves. For the Little River, low-flow days were more likely to occur when the release/inflow ratio was >5.5, and the model used no climate variables (Fig. 4a). However, the Kiamichi River tree showed an interaction between climate and reservoir management variables in a more complex tree (Fig. 4b). Of the six terminal leaves in this tree, three had many low-flow days per month (25.4, 23.8, and 10.5) and three had relatively few (0.18, 0.80, and 0.83). All three terminal leaves with many low-flow days required a low amount of precipitation in the previous month (<5.5 cm) and a release/inflow ratio <0.2. These three leaves were further separated by excessively low precipitation in the previous month (<1.4 cm), low precipitation in the current month (<3.2 cm), or an average high temperature >20.4 °C (Fig. 4b).

DISCUSSION

Here we show that freshwater mussel declines occurred in the Kiamichi River during a multi-year drought, where flows from an upstream impoundment were withheld and

increased the frequency of low water levels known to cause mussel mortality. Because the Little River was managed differently with a minimum release from an upstream impoundment, the occurrence of low-flow days was nearly halved during the multi-year drought. Mussel declines were not observed in the Little River, suggesting that water management practices increased the occurrence of mussel mortality due extreme low-flow conditions and likely lead to the mussel biodiversity declines in the Kiamichi River. While Galbraith et al. (2010) attributed changes in Kiamichi River mussel communities to a combination of drought and management practices, our data presented here suggest that water management practices may have had a stronger role in influencing mussel community changes observed in the Kiamichi River.

Both rivers were sampled for mussels in the 1990s and 2000s, but only the Kiamichi River experienced significant declines in mussel abundance and species richness. In the Kiamichi River we observed a statistically insignificant shift in relative abundance toward thermally tolerant mussel species, but this effect might have been obscured to due a lack of power. Galbraith et al. (2010) found this shift to be statistically significant, but they included more sampling sites than we did in this analysis. Conversely, mussel communities in the Little River experienced little change, over the same 15-year period despite experiencing the same drought, and any trend that was observed was in the opposite direction when compared to the Kiamichi (i.e., shifts in thermally sensitive/tolerant species, Fig. 2c, d).

Our analysis suggests that reservoir management practices can amplify drought conditions in rivers, increasing the occurrence of low-flow days when water levels are already low. Regression tree models showed very different relationships between climate and reservoir management variables for the Little River and Kiamichi River. For the Little River climate variables were not important in predicting the occurrence of low-flow days. This is likely because the driest periods of the year (late summer–early fall) coincide with the highest release/inflow ratios from Pine Creek Lake. Thus, by releasing more water than would naturally be flowing through Pine Creek Lake, the releases decrease the number of low-flow days and maintain mussel habitat. The Little River regression tree model supports this argument: although low-flow days were predicted when the release/inflow ratio was very high (>5.5), a closer look at the data reveals that these months coincided with the lowest inflows to Pine Creek Lake and contributes to the high release/inflow ratio even though the discharge during these months was very low (in these months, inflows were negatively correlated with release/inflow ratio, $r = -0.75$). Therefore, the Little River was already exceptionally dry and experiencing low-flow days despite reservoir releases, not due to a lack thereof.

For the Kiamichi River, many low-flow days per month were only predicted to occur when low precipitation occurred in the previous month, and the release/inflow ratio of Sardis Lake was especially low (<0.2). The three terminal leaves were further separated by exceptionally low precipitation in the previous month, exceptionally low precipitation in the current month, or higher daily maximum air temperatures. Conversely, low-flow days did not occur when precipitation was normal or greater or when the release/inflow ratio was higher than 0.2. Therefore, reduced reservoir releases during dry weather produced low-flow days on the Kiamichi River.

Although the Kiamichi and Little Rivers are similar in climate and in mussel assemblages, our results should be interpreted within some caveats. First, by necessity this was an observational study and not a direct manipulation. Thus, there may be other factors correlated with low-flows that might also have contributed to mussel declines in the Kiamichi River (e.g., corresponding declines in fish host assemblages). Second, the location of dams within each watershed is different. The Sardis Lake dam impounds a tributary of the Kiamichi River, while the Pine Creek Lake dam impounds the mainstem Little River directly (Fig. 1). Although Sardis Lake impounds 30 % of the Kiamichi River watershed, it has a smaller influence on Kiamichi River flows than the Pine Creek Lake dam has on Little River flows. Finally, there are some physical differences between these rivers. Although both rivers originate in and drain the Ouachita uplands and are similar in size and land use (Matthews et al. 2005), our sites on the Kiamichi River are higher in elevation than our sites on the Little River. Thus, there may be some unmeasured geomorphological differences between these rivers at our sampling sites which could influence how mussel communities might be able tolerate droughts (e.g., differences in substrate size that could influence burrowing ability).

Conservation Implications

Conserving mussel biodiversity is important. Freshwater mussels (Unionidae) are already the world's most imperiled faunal group, with nearly 75 % of species listed as threatened or endangered at the state or federal level in the United States. Thirty-five mussel species occur in the Little River and Kiamichi River, including three federally endangered species (*Arkansia wheeleri*, *Leptodea leptodon*, and *Quadrula fragosa*; Galbraith et al. 2008). Mussels provide important ecosystem services such as biofiltration, nutrient recycling, and physical habitat modification (Vaughn 2010). Importantly, studies conducted in these two rivers have shown that mussel biodiversity increases the performance of these ecosystem services by mussel communities (Vaughn et al. 2007; Spooner and Vaughn

2009; Allen and Vaughn 2011; Allen et al. 2012; Spooner and Vaughn 2012). Thus, mussel biodiversity declines may impact ecosystem functioning.

Although minimum flows have been discussed for decades (Gore 1978), large-scale natural or manipulative flow experiments generally manipulate flood occurrence and/or frequency rather than increasing minimum flows (Konrad et al. 2011). Increasing minimum flows has been shown to increase the ecological integrity of benthic aquatic insect and fish communities (Connor and Pflug 2004; Bednarek and Hart 2005; Decker et al. 2008; Bradford et al. 2011), but these studies often restore flows with the purpose of rewetting previously dry reaches instead of increasing existing flows (but see Travnichek et al. 1995). However, in a long-term study Maynard and Lane (2012) found that increased minimum flows led to an increase in macroinvertebrate diversity. Nevertheless, studies investigating the relationship between minimum flows and freshwater mussel diversity are rare in spite of their more imperiled conservation status.

Like other stream organisms, mussels have evolved under and adapted to natural flow regimes (Lytle and Poff 2004). Natural flow regimes have been restored for riparian forests (Rood et al. 2005), and shows promise for promoting native fish existence in competition with non-natives (Gido and Propst 2012). Restoring natural flow regimes to sustain mussels and other stream life is highly desirable because mussel life histories and population success are tightly coupled with hydrology (Rypel et al. 2009; Peterson et al. 2011). However, restoring historic natural flow regimes may not be achievable in many southern rivers due to severely depleted aquifers, human demand, and future climate change. During droughts, both ground and surface water are in high demand, stream flows are already at their lowest levels, and are most susceptible to being reduced to biologically harmful levels by human alteration. Furthermore, climate change models predict increased drought frequency and duration, along with higher summer temperatures for the US southern plains (including the Kiamichi River and Little River basins, Mulholland et al. 1997; IPCC 2007). Nevertheless, for most impounded rivers, we should be able to provide flows that sustain mussels and other aquatic life during droughts, while still meeting basic human needs, and both ecological and policy research should be directed in this area (Richter 2010). Such releases need to be planned carefully based on the dynamics of specific rivers and species life history and habitat needs. For example, hypolimnetic water releases that lead to higher water levels and cooler temperatures during summer months can affect mussel gamete development, parasitism rates, and body condition (Galbraith and Vaughn 2009; Galbraith and Vaughn 2011), and even inhibit mussel reproduction (Layzer et al. 1993; Peterson et al. 2011).

The large-scale impoundment of rivers in North America is largely responsible for mussel declines over the past century, particularly through fragmentation and changes in hydrology (Haag 2012). These impoundments are ubiquitous on the landscape (Poff et al. 2007). While over 800 dams have been removed in the United States (Doyle et al. 2003), more are being constructed in the Southeast, Southwest, and Mountain/Prairie regions (USACE 2010). In these areas, water desired by agriculture and growing urban areas often exceeds supply (OWRB 2012), a situation that will likely be magnified with impending climate change (IPCC 2007; Liu et al. 2012). Our results indicate that we can manage these impoundments to maintain biotic integrity of aquatic ecosystems, in this case the biodiversity of an imperiled fauna. While we cannot control the occurrence, timing, or duration of droughts, we do have the ability to manage our freshwater resources in a responsible way so that drought conditions are not exacerbated.

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