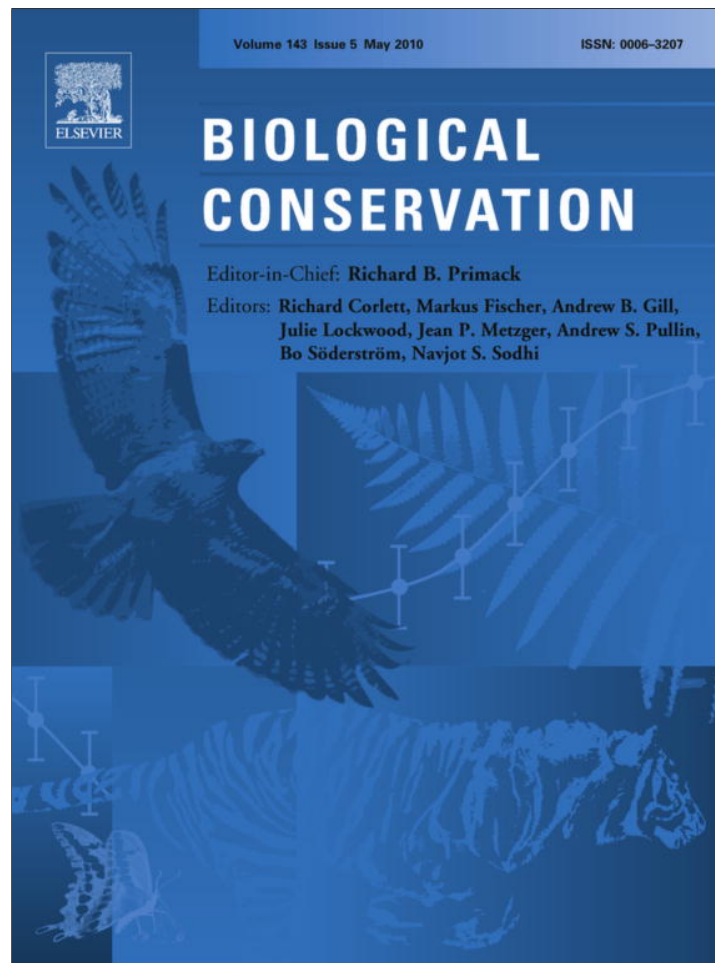


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## Synergistic effects of regional climate patterns and local water management on freshwater mussel communities

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### ABSTRACT

Human alterations to aquatic ecosystems are leading to decreases in species richness and biomass and subsequent changes in community composition. In many cases species losses are non-random: species with traits poorly adapted to the new environmental conditions suffer greater losses. We used long-term data from a southern US river, the Kiamichi River, to evaluate the synergistic effects of regional climate patterns coupled with water management practices on freshwater mussel communities. Mussel communities in the river changed over the 15 year period of this study, with overall densities and species richness decreasing and community structure shifting from assemblages dominated by thermally sensitive to thermally tolerant species. These changes corresponded with a period of very low flows in the river caused by a combination of climate patterns (a regional drought) and local water management practices (decreased reservoir releases). These low flows, coupled with high summer air temperatures, changed the river in many locations from a continuously flowing river to a series of shallow, isolated pools where water temperatures sometimes exceeded 40 °C. Altered conditions led to higher mortality rates of thermally sensitive compared to tolerant species. We predict future shifts in river ecosystem function as mussel communities change in response to changing climate and water management.

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### 1. Introduction

A critical concern in conservation biology is assessing effects of environmental change on biological diversity. Environmental changes lead to non-random species losses and changes in community structure because communities are comprised of species with different traits and thus varying tolerance to environmental stressors (Zavaleta and Hulvey, 2004; Larsen et al., 2005; Schlapfer et al., 2005). Predicted large-scale climate changes will alter environmental gradients with which species interact, and a large amount of research is addressing how species will respond to these changes (IPCC, 2007). Smaller-scale anthropogenic disturbances also change the environmental template against which species traits are expressed (Smart et al., 2006; Lehsten and Kleyer, 2007). Thus, studies addressing climate change need to be able to distinguish organism responses to localized disturbance, such as deforestation and fragmentation, from responses to larger-scale climate change (Schindler, 1997; Xenopoulos et al., 2005). In addition,

studies of biodiversity decline usually have focused on the consequences of species extinctions, but biodiversity losses also include declines in the abundance of common species and shifts in species dominance patterns (Hooper et al., 2005). Common species are typically drivers of ecosystem processes (Dangles and Malmqvist, 2004; Moore, 2006), and such declines can have profound implications for ecosystem function (Merz and Moyle, 2006; Taylor et al., 2006; Moore et al., 2007). Thus, studies addressing how environmental change impacts biodiversity should also look at changes in distribution and abundance of common species.

Freshwater ecosystems, and streams in particular, are losing biodiversity faster than terrestrial or marine systems (Allan and Flecker, 1993; Dudgeon et al., 2006). One of the greatest threats to river systems is the alteration of natural flow regimes (Poff et al., 1997; Lytle and Poff, 2004; Arthington et al., 2006). Changes in the magnitude, frequency, duration, predictability and flashiness of flow due to local water management practices alter macroinvertebrate, fish, and riparian plant communities (Poff et al., 1997; Vaughn and Taylor, 1999; Lytle and Poff, 2004). Climate change also threatens large-scale patterns of freshwater biodiversity (Stenseth et al., 2002; Burgmer et al., 2007). Together, regional climate change and local water management practices have the potential to permanently alter the composition and functioning of many river ecosystems, but the complex nature of communities and environmental gradients makes it

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difficult to accurately predict the outcome of these disturbances (Davis et al., 1998; Botkin et al., 2007).

Freshwater mussels (Bivalvia: Unionoida; hereafter referred to as mussels) are a guild of filter feeding, burrowing bivalves that typically occur as dense, speciose aggregations (mussel beds). Mussels are one of the most threatened faunal groups globally (Lydeard et al., 2004), largely because their life history traits make them highly vulnerable to environmental change. Adult mussels are sedentary; movements are seasonal and on a scale of a few to an estimated maximum of 100 m (Green et al., 1985; Waller et al., 1999). Thus, unlike many stream organisms such as fish and aquatic insects (Townsend, 1989; Matthews, 1998; Matthews and Marsh-Matthews, 2003), mussels have limited refugia from disturbances in streams (e.g. droughts, floods, sedimentation). Further, mussels are very long-lived (10–100 years) with delayed reproduction (typically not reproducing until after age seven, depending on species), leading to long generation times (Anthony et al., 2001; McMahon and Bogan, 2001; Barnhart et al., 2008). Thus, mussels cannot recover rapidly from disturbance. Finally, mussels are thermo-conformers whose physiological processes are constrained by water temperature within species-specific thermal preferences (McMahon and Bogan, 2001; Spooner and Vaughn, 2008). Thus, changes in water temperature can lead to both shifts in community structure and changes in rates and magnitudes of ecological processes provided by mussel communities (Spooner and Vaughn, 2008; Vaughn et al., 2008).

Freshwater mussels are currently experiencing global catastrophic declines in both overall abundance and species richness (Lydeard and Mayden, 1995; Vaughn and Taylor, 1999; Lydeard et al., 2004; Strayer et al., 2004). Mechanisms believed to underlie these declines range from local (riparian clearing, pollution and impacts of invasive species), to regional influences (river fragmentation and altered flow regimes), to global climate change (Strayer, 1999; Watters, 2000; Hastie et al., 2003; Lydeard et al., 2004). These proposed mechanisms are usually addressed and evaluated in isolation, but likely all are important and have simultaneous effects on mussel communities. Here, we use long-term data from a southern US river to evaluate the synergistic effects of regional climate patterns coupled with water management practices on changes in mussel communities.

## 2. Methods

### 2.1. Study area

The Ouachita Uplands covers 34,804 hectares in central and western Arkansas and southeastern Oklahoma, US. This unglaciated region has been isolated from other mountain systems for 225 million years and is a center of speciation for both terrestrial and aquatic organisms, with high numbers of endemic species (Mayden, 1985; Allen, 1990). The region consists of long, parallel, east–west trending mountain ridges and broad valleys with rivers that drain northward to the Arkansas River or southward to the Red River. The steep topography combined with annual precipitation ranging from 100 to 142 cm results in frequent but short-lived spates. The region's rivers are known for their high aquatic diversity, including over 150 species of fishes (Robison and Buchanan, 1988) and 60 species of unionid mussels (Gordon et al., 1979; Vaughn, 2000). They have been far less impacted by human disturbance than many other rivers in North America or Europe, largely because this rural area has, until recently, been relatively unpopulated and undeveloped (Matthews et al., 2005). In fact, this area was selected by The Nature Conservancy as one of the most critical regions in the US for protecting freshwater biodiversity, based largely on its healthy fish and mussel populations (Master et al., 1998).

Rivers in the Ouachita Uplands are considered particularly vulnerable to climate warming (Matthews et al., 2005; Covich et al., 1997; Mulholland et al., 1997). Summer water temperatures in this region often average 35 °C, and can exceed 40 °C in shallow areas, which is at or above the thermal limit of many mussel species and their fish hosts (Spooner and Vaughn, 2008). Mussels and their hosts cannot migrate northward because of prevailing west-to-east major drainages (Matthews and Zimmerman, 1990; Covich et al., 1997). In addition, the Ouachita Uplands' rivers lie approximately 200 miles northeast of the large and growing Dallas-Fort Worth metropolitan area. This area anticipates severe water shortages in the near future, and hopes to divert water from rivers in southeastern Oklahoma (the Little and Kiamichi Rivers) to reservoirs in Texas (Oklahoma Water Resources Board, 2000a,b, 2002). Depending on regional climate patterns, water transfer and associated reservoir management have the potential to severely alter stream hydrology and impact mussel communities.

Our study focused on the Kiamichi River, a major tributary of the Red River in southeastern Oklahoma. This relatively pristine river is 272 km long with a drainage area of 4660 km<sup>2</sup>. It is typically clear and rocky bottomed in the headwaters, becoming sluggish in its downstream reaches where it is bordered by lowlands and swamps (Matthews et al., 2005). The river is influenced by two impoundments (Fig. 1). A major tributary, Jackfork Creek, provides 30% of the inflow to the river and is impounded by Sardis Reservoir. Construction of this reservoir began in 1975 and was completed in 1983 (Oklahoma Water Resources Board, 2000a). The lower Kiamichi River is impounded by Hugo Reservoir (Galbraith et al., 2008).

### 2.2. Mussel communities and thermal guilds

Mussels often occur in multi-species, aggregated assemblages called mussel beds. In the Ouachita Uplands, mussel beds can range from 50 to 5000 m<sup>2</sup> with densities in beds typically 10–100 times greater than areas outside of beds (Spooner and Vaughn, 2009). Although beds are speciose, with some containing greater than 20 species (Vaughn and Spooner, 2006), mussel species within beds are log-normally distributed with a few dominant species comprising most of the biomass and the majority much more rare (Spooner and Vaughn, 2009). Mussel species in these beds also vary in multiple traits, ranging from overall size and shell morphology to the spacing of cilia on the gills (Galbraith et al., 2009), to burrowing behavior (Allen and Vaughn, 2009), and importantly, thermal performance. Mussels are thermo-conformers whose physiological processes are constrained by water temperature (McMahon and Bogan, 2001). Spooner and Vaughn (2008) performed laboratory experiments examining the effects of a range of naturally occurring temperatures (5 °C, 15 °C, 25 °C, 35 °C) on the condition (measured as metabolic rates and tissue glycogen concentration) and the rates of ecosystem processes (filtration, biodeposition of organic material, nutrient excretion) performed by eight common species in Kiamichi River mussel beds (Table 1). They found that mussel species could be placed into two general guilds based on their condition and performance at warm temperatures (35 °C). *Thermally tolerant* or *warm* species were in good condition at warm temperatures. They increased their feeding activities and in turn provided more excreted nutrients and biodeposits to the stream ecosystem. In contrast, *thermally sensitive* or *cool* species were in poorer physiological condition at warm temperatures, decreased their feeding rates, and generally contributed less organic material to the ecosystem (Spooner and Vaughn, 2008).

### 2.3. Mussel sampling

We sampled mussels in the early 1990s (1990–1992) and 2000s (2003–2005) from 10 Kiamichi River sites (Fig. 1; Vaughn and Pyr-

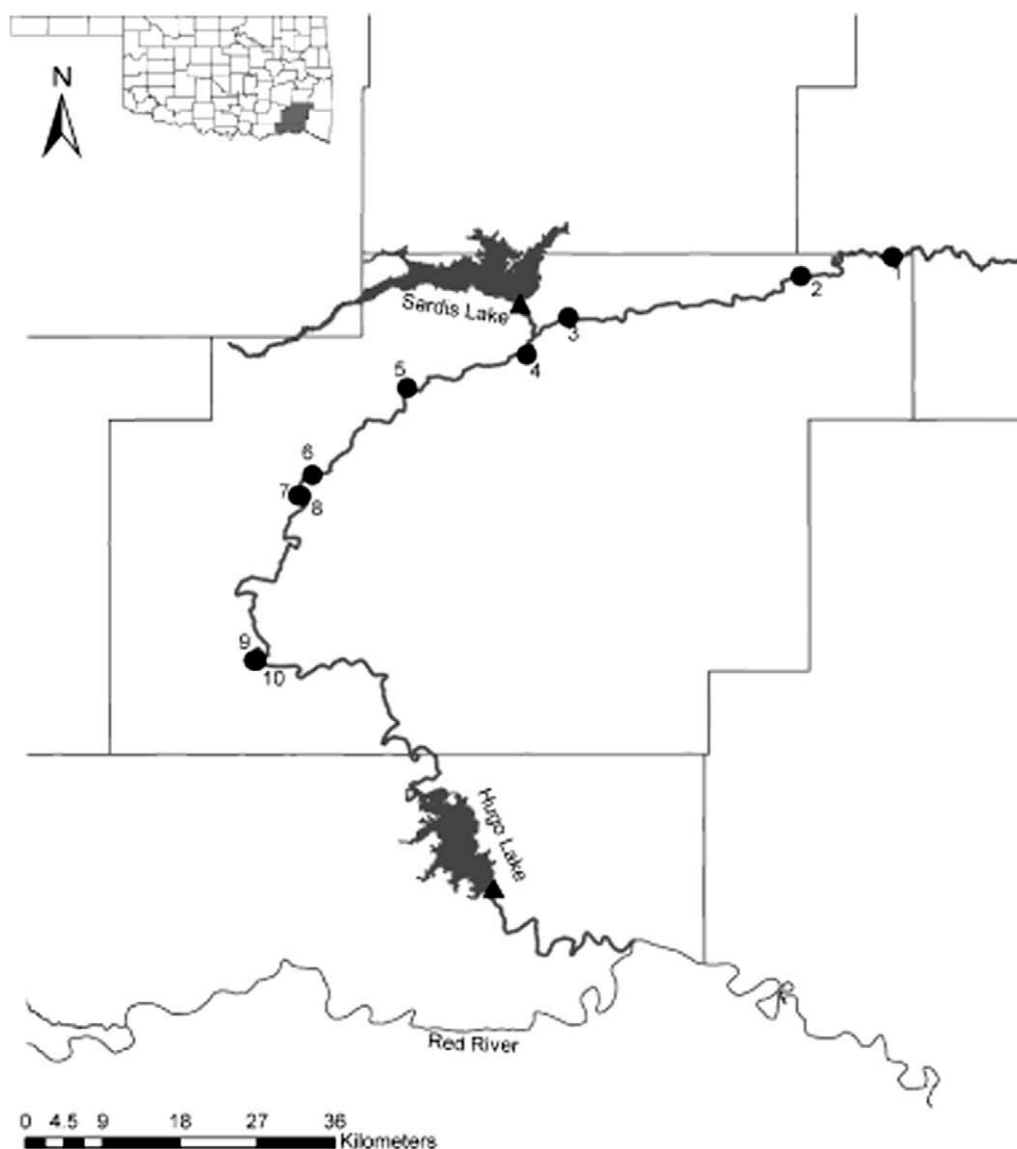


Fig. 1. Sample sites (circles) and dams (triangles) in the Kiamichi River in southeastern Oklahoma, USA.

Table 1

Phylogenetic classification (Graf and Cummings, 2006), mean body size of individuals collected in time searches in 2004 and thermal tolerance groupings (Spooner and Vaughn, 2008) of common mussel species in the Kiamichi River.

Species	Tribe	Body size (length in mm)	Delta $Q_{10}$ <sup>a</sup>	Thermal guild
<i>Actinonaias ligamentina</i>	Lampsilini	116.0 (0.8)	-0.83	Sensitive
<i>Lampsilis cardium</i>	Lampsilini	105.2 (2.0)	-1.45	Sensitive
<i>Quadrula pustulosa</i>	Quadrulini	61.4 (1.4)	-0.26	Sensitive
<i>Truncilla truncata</i>	Lampsilini	55.8 (1.8)	-0.14	Sensitive
<i>Amblema plicata</i>	Amblemini	96.9 (0.5)	0.08	Tolerant
<i>Fusconaia flava</i>	Pleurobemini	72.6 (0.9)	0.59	Tolerant
<i>Megaloniais nervosa</i>	Amblemini	157.1 (2.0)	0.40	Tolerant
<i>Obliquaria reflexa</i>	Lampsilini	56.3 (1.1)	0.15	Tolerant

<sup>a</sup> Delta  $Q_{10}$  =  $Q_{10}$  anabolism -  $Q_{10}$  catabolism at 35°C.  $Q_{10}$  anabolism rates were determined from rates of oxygen consumption and  $Q_{10}$  catabolism rates were determined from  $NH_3$  excretion rates. Data are from Spooner and Vaughn (2008).

on, 1995). Sites 1–3 were above a major tributary to the river (Jack Fork Creek) and sites 4–10 were downstream of this tributary but above a mainstream impoundment (Hugo Reservoir). The river is smaller and higher gradient above Jack Fork Creek (Matthews et al., 2005). While 15 years may seem like a long time between sampling periods, this is an appropriate sampling interval to detect

community changes in these long-lived, sedentary species with delayed reproduction (Heller, 1990). For long-lived organisms with slow growth and sporadic reproduction, sampling too frequently can result in serially correlated data and false conclusions about rates of change (Schroeter et al., 1993). For example, sampling an organism that lives 60 years every 15 years represents one quarter



of its life span and is thus analogous to sampling an annual insect or plant every 3 months. In addition, mussels are extremely sensitive to handling, which can slow their growth and impact reproduction and should not be sampled any more than necessary (Cope and Waller, 1995; Monroe and Newton, 2001).

Both quantitative (quadrat excavation) and semi-quantitative (timed searches) sampling was conducted at each site for each time period (Strayer and Smith, 2003). We excavated 15, randomly-placed, 0.25 m<sup>2</sup> quadrats per site to a depth of approximately 15 cm (Vaughn et al., 1997). Timed searches consisted of at least 2 h of searching for mussels visually and by feel; SCUBA was used in deeper areas. Quadrat sampling always preceded timed searches. Live mussels were collected, brought to shore and identified, and returned to their original position in the streambed.

At a single site (site 7, Fig. 1) on August 28, 2000, we examined the relationship between mussel mortality, water depth and water temperature. We chose this site because it contained a large, diverse mussel bed and is representative of other “typical” mussel beds in the river (Vaughn and Pyron 1995). We counted live and freshly dead (shell with some tissue remaining) mussels in 40, 0.25 m<sup>2</sup> quadrats and measured water depth. We excavated quadrats to a depth of 15 cm, thus live and freshly dead mussels should have been equally detectable. For 25 quadrats containing freshly dead mussels, we also measured water temperature at the sediment–water interface using a Reotemp<sup>®</sup> Digital TM99-A thermometer. All water temperature measurements were point measurements taken from the center of the quadrats and were made within a few hours of midday.

#### 2.4. Climate, flow and water management data

We obtained regional temperature and precipitation data from the Oklahoma Mesonet ([www.mesonet.org](http://www.mesonet.org)), a series of tower-based continuous-recording weather stations, and the Oklahoma Climatological Survey ([climate.ok.gov](http://climate.ok.gov)), the operators of the Oklahoma Mesonet. These estimates of temperature and precipitation were collected by averaging data from nine Mesonet monitoring sites across four counties (Leflore, Latimer, McCurtain and Pushmataha) in southeastern Oklahoma.

Kiamichi River discharge data were from USGS gauging station 07335790 near Clayton, OK, which began operation in 1980 ([waterdata.usgs.gov/ok](http://waterdata.usgs.gov/ok)). This is the closest gauging station to Sardis Reservoir. During our sampling we observed very low flows in the river, which corresponded with mussel mortality events (Fig. 2). To examine the frequency of these events, we first examined discharge patterns in the river from 1980–2005. We found that <5% of all flows across this time periods were below 1 ft<sup>3</sup> s<sup>-1</sup> (0.028 m<sup>3</sup> s<sup>-1</sup>), and that this discharge rate corresponded with

dates where we had observed that sections of the river still contained water but were pooled and some sections were non-flowing. Thus, we set this as our biologically relevant threshold for significantly low flows.

Data on the amount of water released from Sardis Reservoir into the Kiamichi River were obtained from the Army Corp of Engineers ([www.swt-wc.usace.army.mil/SARDcharts.html](http://www.swt-wc.usace.army.mil/SARDcharts.html)). Reservoir release data were not available before 1995. Thus, we examined data for the entire period of record (1995–2005) and from the beginning of the drought onward (1998–2005).

#### 2.5. Data analyses

We compared differences in mussel density and species richness between the historical (1990s) and recent (2000s) sampling periods with ANOVA. We then grouped the most abundant mussel species into the two thermal guilds described above (Table 1) and used chi-square to compare the proportion of the mussel community comprised of these guilds historically and in the present. Using the data collected from site 7 in 2000, we used regression to examine the relationship between water depth and water temperature and water depth and mussel mortality. We also used regression to determine if there were any *a priori* differences in the depth distribution of thermally tolerant versus thermally sensitive species. To do this, we tallied all of the live and dead mussels within each quadrat and grouped them according to their thermal tolerance and regressed this against the depth of the quadrat. We again assigned species to thermal guilds, and used chi-square to examine the relationship between thermal guild and mussel mortality. We examined the amount of water released downstream into the Kiamichi River relative to that coming into the reservoir (reservoir release/inflow) over time with regression. All statistical analyses were performed with SPSS (SPSS Inc., Chicago, Illinois, USA) except chi-square analyses were done by hand. Mesonet temperature and precipitation data were smoothed with a loess smoothing function in Sigmaplot version 10.0 (Systat Software Inc., Chicago, Illinois, USA) using the software's default parameters (first degree polynomial, sampling proportion = 0.1).

### 3. Results

During the late 1990s–2005, southeastern Oklahoma experienced a severe drought. While temperature averaged across the three summer months was within the variation of the long term record (Fig. 3), August of 2000 was the driest August on record since the early 1940s, precipitation statewide broke the record low of 1936 (Oklahoma Climatological Survey, 2008), and 20% of days had discharge below 1 ft<sup>3</sup> s<sup>-1</sup>. It was also one of the hottest Augusts on record since the very early 1980s and the Palmer

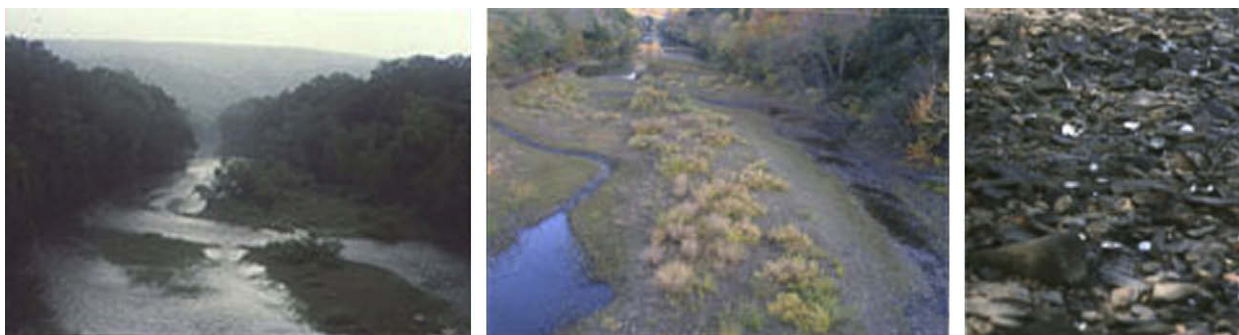
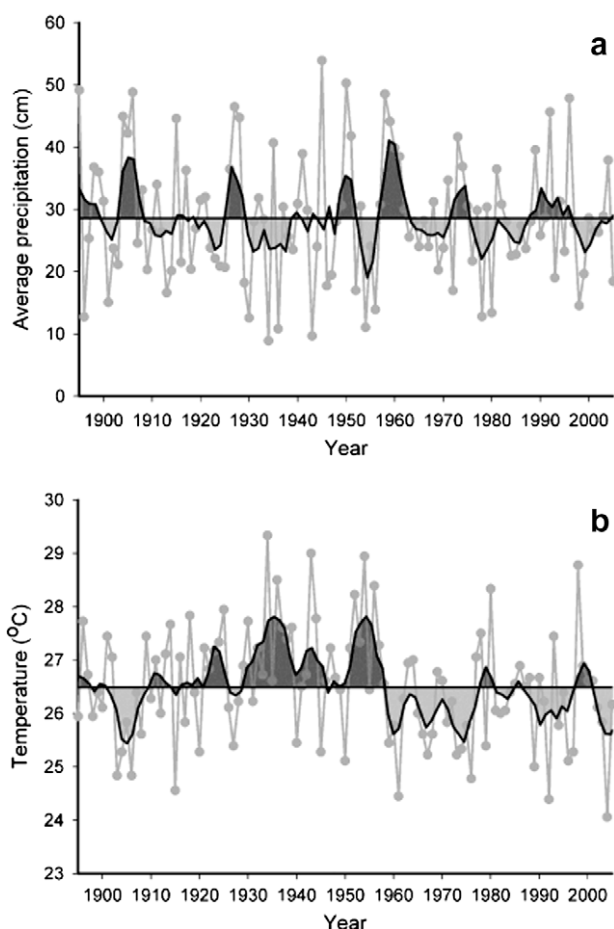


Fig. 2. Left: photograph of the main channel of the Kiamichi River under normal flow conditions. Middle: the same location during drought conditions, showing isolated pools and dry stretches. Right: close up of a dry stretch showing dead mussels. Photos by Caryn Vaughn and Heather Galbraith.

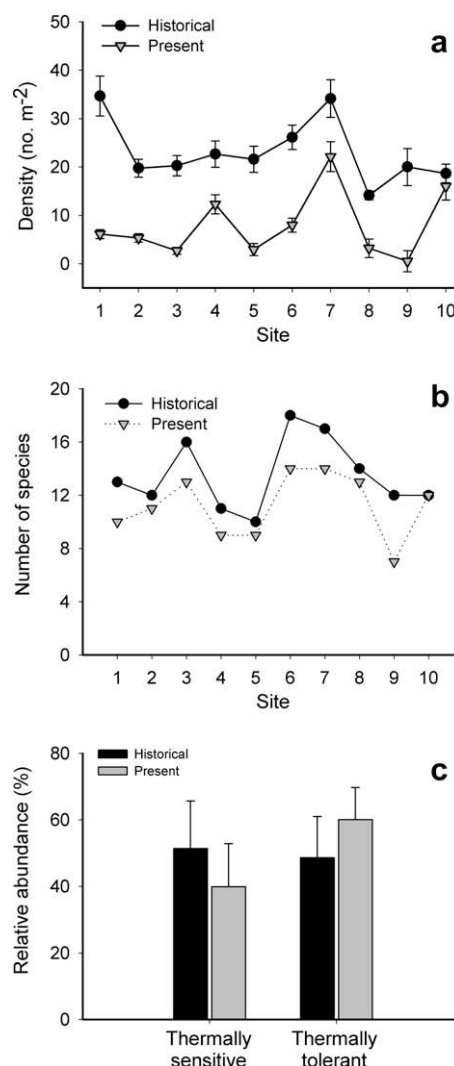


**Fig. 3.** Trends (averages and averages smoothed over time using a LOESS smoothing model) in (a) summer (June–August) precipitation and (b) summer (June–August) temperature in southeastern Oklahoma. Points represent the summer average. The straight line dividing each graph represents long-term average precipitation (a) and temperature (b) from 1895 to 2007. Dark shaded areas above this line represent periods of either high temperature or precipitation while light shaded areas below the line represent periods of low temperature and precipitation. Data courtesy of the Oklahoma Climatological Survey and the Oklahoma Mesonet. Data are regional averages across four counties and nine mesonet monitoring stations.

Drought Index classified southern and southeastern Oklahoma as under mild to moderate drought conditions (OWRB, 2000b).

Mean mussel density in the Kiamichi River decreased by almost 65% between the two time periods, from 23.2 mussels  $m^{-2}$  ( $\pm 2.1$  SE) to 7.9 mussels  $m^{-2}$  ( $\pm 2.2$  SE) ( $F_{(1,18)} = 25.58$ ,  $p < 0.001$ ). Decreases occurred across all sites (Fig. 4a), and included both rare and common species. Species richness decreased from a historical mean richness of 13 ( $\pm 0.76$ ) to a present mean richness of 11 ( $\pm 0.76$ ) ( $F_{(1,18)} = 4.1$ ,  $p = 0.06$ ) and richness decreased across all sites but one (Fig. 4b). We also saw shifts in community composition, with thermally tolerant species comprising a larger proportion of the community over the time span of our study (Fig. 4c; ( $\chi^2_{(1)} = 5.26$ ,  $p < 0.05$ ).

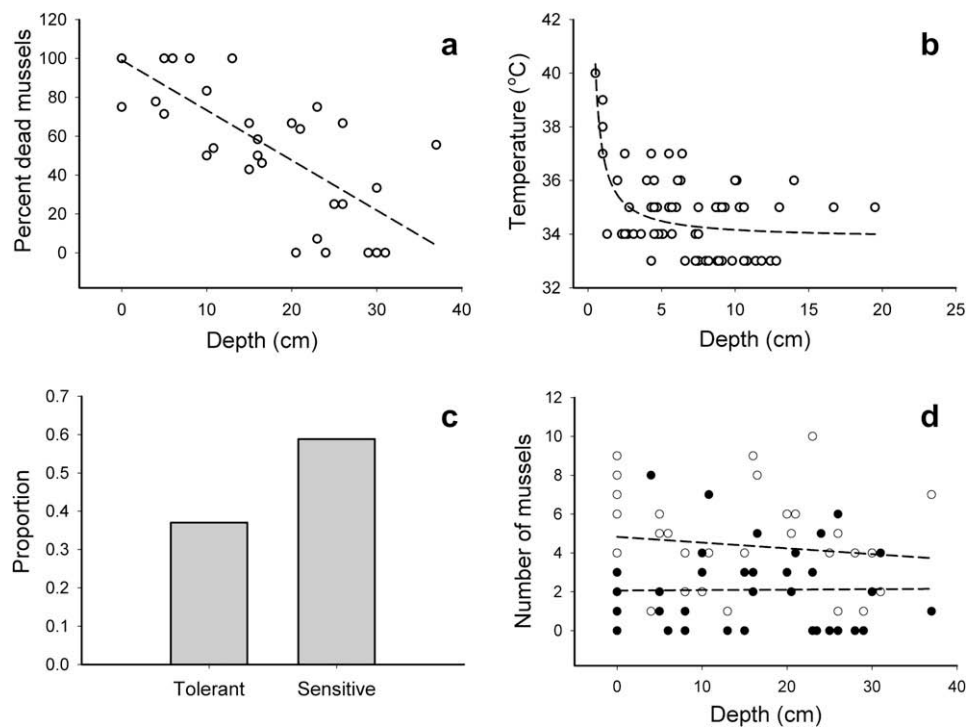
At site 7 in 2000, we found significant negative relationships between water depth and mussel mortality (Fig. 5a;  $r^2 = 0.62$ ,  $F_{(1,37)} = 62.29$ ,  $p < 0.001$ ) and water depth and water temperature at the sediment water interface where freshly dead mussels were found (Fig. 5b;  $r^2 = 0.38$ ,  $F_{(1,67)} = 43.13$ ,  $p < 0.001$ ). We also found that quadrats contained proportionally more live thermally tolerant species ( $\chi^2_{(1)} = 2.16$ ,  $p = 0.02$ ) and more dead thermally sensitive species ( $\chi^2_{(1)} = 4.01$ ,  $p = 0.037$ ) than expected by chance (Fig. 5c). We did not find any relationship between mussel thermal tolerance and depth distribution (Fig. 5d; thermally sensitive:



**Fig. 4.** Historical and recent mussel communities. (a) Mean ( $\pm$ SE) mussel densities from quadrats at 10 monitoring sites in 1990–1992 and 2003–2005; (b) species richness from timed searches at the 10 monitoring sites in 1990–92 and 2003–05; and (c) river-wide shifts in species composition from 1990–92 to 2003–05 (mean relative abundance  $\pm$  SE).

$r^2 = 0.00$ ,  $F_{(1,38)} = 0.69$ ,  $p = 0.41$ ; thermally tolerant:  $r^2 = 0.00$ ,  $F_{(1,38)} = 0.01$ ,  $p = 0.94$ ), suggesting that mussels were evenly distributed across depths, and that mussel death was indeed due to their thermal traits, not their depth preference.

Periodic droughts are normal and cyclical in the US southern plains (Matthews et al. 2005). The 15 year time span of our study encompassed both a wet and dry period (Fig. 3), with the years from 1998 to 2005 exhibiting above-average August temperatures and below average August precipitation, with mean annual precipitation in recent history decreasing over time ( $r^2 = 0.22$ ,  $F_{(1,9)} = 3.88$ ,  $p = 0.08$ ). Correspondingly, we observed a large peak in the number of days with very low flow during the late 1990s and early 2000s (Fig. 6a). Low flows were exacerbated by reservoir management practices. Reservoir release data from Sardis Reservoir began in 1995. During the drought (1998–2005), the amount of water released downstream to the Kiamichi River compared to the amount received by Sardis Reservoir during summer months showed a progressively decreasing trend over time (Fig. 6b; 1995–2005,  $r^2 = 0.11$ ,  $F_{(1,9)} = 2.21$ ,  $p = 0.17$ ; 1998–2005,  $r^2 = 0.633$ ,  $F_{(1,6)} = 13.07$ ,  $p = 0.011$ ). The periods of low release occurred during the warmest time of year (summer) (Fig. 6c).



**Fig. 5.** Relationship between water depth, water temperature and mussel mortality at site 7 in August 2000. (a) Relationship between water depth and percent mussel mortality; (b) relationship between water depth and water temperature; (c) proportion of dead mussels in thermally tolerant vs. thermally sensitive guilds found in quadrats; and (d) relationship between quadrat depth and number of mussels in each thermal guild. Closed circles represent thermally tolerant species and open circles represent thermally sensitive species.

#### 4. Discussion

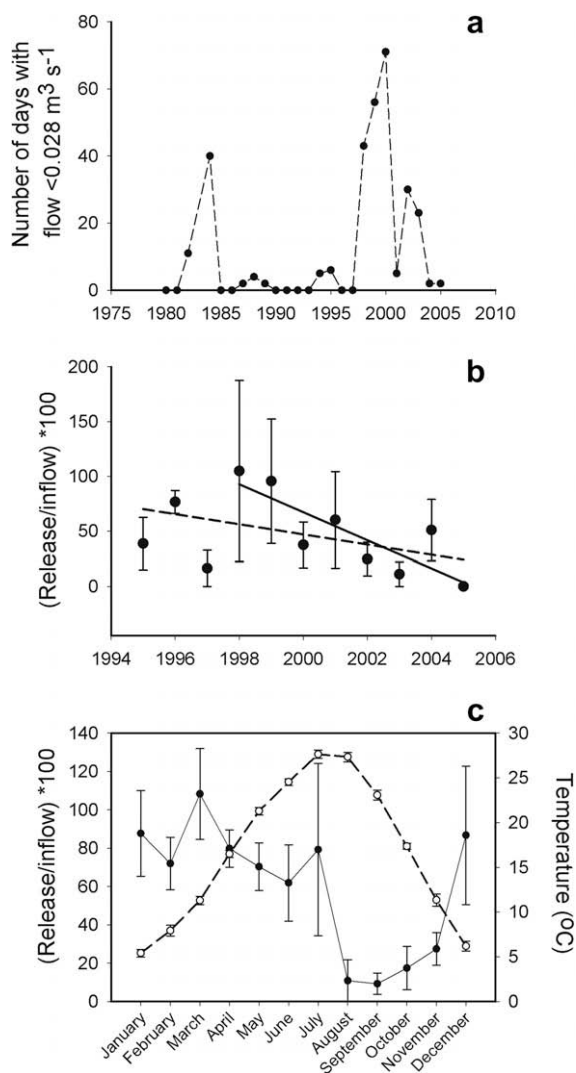
Mussel communities in the Kiamichi River changed over the 15 year period of this study, with overall abundance and species richness decreasing and relative abundance patterns shifting from assemblages dominated by thermally sensitive to thermally tolerant species. These changes corresponded with a period of very low flows in the river, which appear to have been caused by a combination of climate patterns (a regional drought; Figs. 3 and 6a) and local water management practices (reduced reservoir releases; Fig. 6b). These low flows coupled with high summer air temperatures (Fig. 3), changed the Kiamichi River in many locations from a continuously flowing river to a series of shallow, isolated pools where water temperatures sometimes exceeded 40 °C (Figs. 2, 5b; Spooner and Vaughn, 2000). Mussels are thermo-conformers with different strategies for avoiding physiological temperature stress. More mobile species can move to deeper regions of a stream reach to survive the heat, while others “clam up” and become metabolically less active while catabolizing their energy reserves (McMahon and Bogan, 2001). However, regardless of their heat-avoiding strategy, no mussel can survive an extended amount of time in an isolated pool at high temperatures, low dissolved oxygen, and often high ammonia levels (Gagnon et al., 2004; Cherry et al., 2005; Haag and Warren, 2008). We believe that thermal stress associated with low water levels is one of the proximate causes underlying the declines we observed in mussel abundance and species richness, and our observation that mussel mortality was related to water depth and thus temperature supports this premise (Fig. 5). In addition, we observed that once mussels began dying in these isolated pools (Fig. 2), tissue decay led to large nutrient pulses (Vaughn et al., 2008), algal blooms, lowered dissolved oxygen levels, and thus further mussel mortality.

Species traits should match the environmental landscape in which they evolved (Poff, 1997; McGill et al., 2006). Present mussel

community composition should be a reflection of the environmental conditions under which species evolved, and reflect historical patterns of environmental change. Therefore, present mussel communities in the Kiamichi River are comprised of the species that have survived past disturbance events. However, under changing environmental conditions, species losses should occur non-randomly based on the distinct traits of individual species (Zavaleta and Hulvey, 2004; Schlapfer et al., 2005; Cross and Harte, 2007), and our results support this premise. As described earlier, Spooner and Vaughn (2008) found that mussel species in the Kiamichi River could be assigned to two thermal guilds based on differences in resource acquisition and assimilation rates when acclimated to different temperatures. Thermally tolerant species continue to grow at warm summer water temperatures, whereas thermally sensitive species become stressed and catabolize their own tissue at temperatures between 25 °C and 35 °C. Our data show that mussel mortality was related to thermal tolerance, with higher mortality rates for sensitive as compared to tolerant species (Fig. 5). We believe that over the period of the drought, this difference in mortality rates led to a river-wide shift in species composition from thermally sensitive dominated to thermally tolerant dominated mussel communities (Fig. 4c).

Species range shifts in response to climate change have occurred throughout the earth's history, and in recent years many species have been expanding their ranges in response to increasing temperatures (Parmesan and Yohe, 2003; Hickling et al., 2006). In freshwater systems, most concern has been for coldwater species at high latitudes and/or altitudes because it is predicted they will not have the physiological tolerance to withstand warmer water temperatures (Wrona et al., 2006). However, freshwater species vary widely in their physiological responses to temperature, thus they should also vary in their response to changing climates, regardless of their latitude or altitude of origin, or whether they are coldwater or warmwater species (Heino et al., 2009). If regional





**Fig. 6.** Historical and present trends in discharge and temperature in the Kiamichi River. (a) Number of days with very low flow (defined as discharge less than  $0.028 \text{ m}^3 \text{ s}^{-1}$  ( $1 \text{ ft}^3 \text{ s}^{-1}$ )) from USGS station number 07335790 ([waterdata.usgs.gov/ok/nwis/rt](http://waterdata.usgs.gov/ok/nwis/rt)) from 1980 (date station began operation) to 2005. (b) Mean summer (May–September) Sardis Reservoir release/inflow ( $\pm$ SE) ([www.swt-wc.usace.army.mil/SARDcharts.html](http://www.swt-wc.usace.army.mil/SARDcharts.html)); Hatched line, 1995–2005,  $r^2 = 0.11$ ,  $F_{(1,9)} = 2.21$ ,  $p = 0.17$ ; solid line, 1998–2005,  $r^2 = 0.633$ ,  $F_{(1,6)} = 13.07$ ,  $p = 0.011$ . (c) Mean monthly Sardis Reservoir release/inflow ( $\pm$ SE) and mean monthly air temperature ( $\pm$ SE) from 1995–2005. Data courtesy of the Oklahoma Mesonet, USGS and the US Army corps of engineers.

climate patterns differentially impact thermally sensitive species, we would expect these patterns to be most pronounced on the periphery of their southern distribution. For our system, observed dominance shifts and published range maps overall supported this prediction. *Amblema plicata*, *Megaloniais nervosa*, *Fusconaia flava* and *Obliquaria reflexa*, classified as thermally tolerant (Table 1), increased in relative dominance in our study. All four of these species have ranges that extend well into Oklahoma and southward into Texas (Parmalee and Bogan, 1998). In contrast, three of the thermally sensitive species in our study, *Actinonaias ligamentina*, *Lampsilis cardium* and *Quadrula pustulosa*, are at the southern and western edge of their range in the Kiamichi River (Parmalee and Bogan, 1998). Only *Truncilla truncata*, a thermally sensitive species with a range extending into Texas, did not fit that pattern. Rigorous testing this hypothesis will require distribution data at larger scales than were available for this study.

Other studies have observed similar decreases in mussel density and richness in both rare and abundant species following se-

vere droughts (Gagnon et al., 2004; Golladay et al., 2004; Haag and Warren, 2008). For example, Gagnon et al. (2004) observed shifts in community composition in the tributaries of the Flint River, Georgia, where generalist species became dominant following drought. However, these results are contradictory to work performed by Haag and Warren (2008) who found that species composition did not change in relation to drought in Alabama and Mississippi. Hastie et al. (2003) reviewed the effects of climate change on the freshwater mussel species *Margaritifera margaritifera* and predicted changes in mussel communities similar to those observed in our study. They noted that a change in extreme thermal events due to global warming is likely to be the major factor leading to declines in freshwater mussel communities and predicted that altered precipitation may lead to changes in mussel recruitment.

In the southern US, low-flow periods usually occur in the summer and can be due to natural droughts (Matthews et al., 2005), human water management, or a combination of both factors. Drought is a normal feature of long-term climate patterns in the Kiamichi River watershed (Fig. 3) and mussels there obviously evolved under cyclical wet and dry periods. However, we believe the drought conditions experienced by mussels during this study were exacerbated by human management of river flows. Sardis Lake, an impoundment of a tributary to the Kiamichi River, normally provides 30% of the inflow into the river (Fig. 1; Matthews et al., 2005). Our study period corresponded with the first drought period experienced by the Kiamichi River since the completion of Sardis Lake dam in 1983 (OWRB, 2000a). Sites 1–3, above the reservoir, are higher gradient and normally shallower than sites downstream of the reservoir and thus should be more susceptible to drought conditions than deeper downstream sites which, without water management, should hold water longer. Yet, we observed declines of thermally sensitive species throughout the river, indicating an interaction of both climate and water management. Discharge data for the Kiamichi River below Sardis Reservoir are not available prior to 1980, thus it is difficult to make an unequivocal link between changes in mussel communities and water management. Nonetheless, our analysis of reservoir release volumes demonstrated that: (1) managers withheld the largest volumes of water during the time of year that the smallest volumes of inflow were entering the system, thus exacerbating already hot and dry conditions (Fig. 6c); and (2) there was a trend for managers to release progressively less water to the river downstream as the drought continued (Fig. 6b). We believe this combination of natural drought and human management led to the creation of isolated pools, resulting in high summer water temperatures and subsequent species-specific mussel mortality rates. Factors other than drought have likely partially contributed to mussel declines and species dominance shifts in our study. For example, long-term declines in mussel species richness have also been linked to changing land use practices and increased nitrogen concentration (Bauer, 1988; Arbuttle and Downing, 2002; Poole and Downing, 2004). Over the course of our study we observed siltation of mussel beds from riparian clearing, pollution, gravel mining, and driving vehicles across mussel beds for recreation, all of which locally impacted mussels (Vaughn and Pyron, 1995; Galbraith et al., 2008). However, these factors were highly localized and we doubt that they led to the large-scale, river-wide patterns we observed showing shifts in mussel communities that were related to their thermal tolerance. In addition, mussels have a larval stage (glochidium) that is an obligate ectoparasite on fishes; thus, anything impacting fish host populations would also impact mussel populations. However, fish populations in the Kiamichi River are resilient, can more easily seek refuge from drought, and appear to have been relatively unimpacted by the drought or landuse changes (Pyron et al., 1998; Matthews and Marsh-Matthews, 2003).



#### 4.1. Conservation implications

We should be concerned about the actual losses of mussels observed in this study, and the potentially larger losses that may be looming worldwide in the future with climate change and human demand for water. Not only are mussels a globally imperiled fauna, recent work has shown that they perform important functions in stream ecosystems, linking the benthic and pelagic compartments through their filtering activities, recycling nutrients, stimulating primary and secondary production, and providing habitat for other organisms (Howard and Cuffey, 2006; Spooner and Vaughn, 2006; Aldridge et al., 2007; Christian et al., 2008; Vaughn et al., 2008). The amount of material that mussels can process is, in general, linearly related to their biomass (Vaughn et al., 2004). We observed consistent declines in mussel abundance and thus biomass, and similar trends have been documented across the US (Neves et al., 1997; Strayer et al., 2004) and globally (Lydeard et al., 2004). This loss of filter feeding biomass portends a loss of ecological function for rivers where mussels were once abundant.

We also should be concerned about shifts in mussel species dominance patterns, and potential shifts in species overall ranges. Because mussels perform ecosystem processes at different rates depending on their physiological tolerances and optima, species composition and environmental conditions interact to determine the magnitude of ecosystem processes provided by mussels to the stream ecosystem (Spooner and Vaughn, 2008; Vaughn et al., 2008). Evidence from field and laboratory experiments indicates that thermally tolerant and thermally sensitive mussel communities are contributing differently to ecosystem function (Spooner and Vaughn, 2008; Vaughn et al., 2008), and we predict shifts in ecosystem function in the future as communities change in response to changing climate and water management.

Climate change models predict increased drought and higher summer temperatures for the US southern plains (including the Kiamichi River basin). These models predict as much as a 4 °C increase in seasonal air temperature (Mulholland et al., 1997; IPCC, 2007), accompanied by increases in frequency and intensity of severe thunderstorms separated by much longer drought periods. At the same time, human demand for water from this rural region is growing almost exponentially and there are plans to divert water from the Kiamichi and other rivers in the region to large metropolitan areas to meet human demand (Oklahoma Water Resources Board, 2000a,b, 2002). Depending on actual drought conditions and how proposed water diversions and reservoir releases are managed, this combination of predicted regional climate patterns and local, human management of water resources has the potential to alter mussel communities and freshwater communities in general. While we cannot control the frequency or severity of droughts, we can manage water resources so that drought conditions are not exacerbated.

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#### References

- Aldridge, D.C., Fayle, T.M., Jackson, N., 2007. Freshwater mussel abundance predicts biodiversity in UK lowland rivers. *Aquatic Conservation-Marine and Freshwater Ecosystems* 17, 554–564.
- Allan, J.D., Flecker, A.S., 1993. Biodiversity conservation in running waters. *BioScience* 43, 32–43.
- Allen, D.C., Vaughn, C.C., 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. *Journal of the North American Benthological Society* 28, 93–100.
- Allen, R.T., 1990. Insect endemism in the Interior Highlands of North America. *Florida Entomologist* 73, 539–569.
- Anthony, J.L., Kesler, D.H., Downing, W.L., Downing, J.A., 2001. Length-specific growth rates in freshwater mussels (*Bivalvia*: Unionidae): extreme longevity or generalized growth cessation? *Freshwater Biology* 46, 1349–1359.
- Arbuckle, K.E., Downing, J.A., 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 310–316.
- Arthington, A.H., Bunn, S.E., Poff, N.L., Naiman, R.J., 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications* 16, 1311–1318.
- 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.
- Bauer, G., 1988. Threats to the fresh-water pearl mussel *Margaritifera margaritifera* in central Europe. *Biological Conservation* 45, 239–253.
- Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., Stockwell, D.R.B., 2007. Forecasting the effects of global warming on biodiversity. *BioScience* 57, 227–236.
- Burgmer, T., Hillebrand, H., Pfenninger, M., 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia* 151, 93–103.
- Cherry, D.S., Scheller, J.L., Cooper, N.L., Bidwell, J.R., 2005. Potential effects of Asian clam (*Corbicula fluminea*) die-offs on native freshwater mussels (Unionidae) I: water-column ammonia levels and ammonia toxicity. *Journal of the North American Benthological Society* 24, 369–380.
- Christian, A.D., Crump, B.G., Berg, D.J., 2008. Nutrient release and ecological stoichiometry of freshwater mussels (Mollusca:Unionidae) in two small, regionally distinct streams. *Journal of the North American Benthological Society* 27, 440–450.
- Cope, W.G., Waller, D.L., 1995. Evaluation of freshwater mussel relocation as a conservation and management strategy. *Regulated Rivers: Research and Management* 11, 147–155.
- Covich, A.P., Fritz, S.C., Lamb, P.J., Marzolf, R.D., Matthews, W.J., Poiani, K.A., Prepas, E.E., Richman, M.B., Winter, T.C., 1997. Potential effects of climate change on aquatic ecosystems of the Great Plains of North America. *Hydrological Processes* 11, 993–1021.
- Cross, M.S., Harte, J., 2007. Compensatory responses to loss of warming-sensitive plant species. *Ecology* 88, 740–748.
- Dangles, O., Malmqvist, B., 2004. Species richness-decomposition relationships depend on species dominance. *Ecology Letters* 7, 395–402.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391, 783–786.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Leveque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81, 163–182.
- 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.
- Galbraith, H.S., Spooner, D.E., Vaughn, C.C., 2008. Status of rare and endangered freshwater mussels in southeastern Oklahoma. *Southwestern Naturalist* 53, 45–50.
- Galbraith, H.S., Frazier, S.E., Allison, B., Vaughn, C.C., 2009. Comparison of gill surface morphology across a guild of suspension-feeding unionid bivalves. *Journal of Molluscan Studies* 75, 103–107.
- Golladay, S.W., Gagnon, P., Kearns, M., Battle, J.M., Hicks, D.W., 2004. Response of freshwater mussel assemblages (*Bivalvia*: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. *Journal of the North American Benthological Society* 23, 494–506.
- Gordon, M.E., Kraemer, L.R., Brown, A.V., 1979. Unionaceae of Arkansas: historical review, checklist, and observations on distributional patterns. *Bulletin of the American Malacological Union* 1979, 31–37.
- Graf, D.L., Cummings, K.W., 2006. Palaeoheterodont diversity (Mollusca: Trigonoida + Unionoida): what we know and what we wish we knew about freshwater mussel evolution. *Zoological Journal of the Linnean Society* 148, 343–394.
- Green, R.H., Singh, S.M., Bailey, R.C., 1985. Bivalve molluscs as response systems for modeling spatial and temporal environmental patterns. *The Science of the Total Environment* 46, 147–169.
- Haag, W.R., Warren, M.L.J., 2008. Effects of severe drought on freshwater mussel assemblages. *Transactions of the American Fisheries Society* 137, 1165–1178.

- Hastie, L.C., Cosgrove, P.J., Ellis, N., Gaywood, M.J., 2003. The threat of climate change to freshwater pearl mussel populations. *Ambio* 32, 40–46.
- Heino, J., Virkkala, R., Toivonen, H., 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* 84, 39–54.
- Heller, J., 1990. Longevity in molluscs. *Malacologia* 31, 259–296.
- Hickling, R., Boy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distribution of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12, 450–455.
- Hooper, D.U., Chapin, F.S.I., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35.
- Howard, J.K., Cuffey, K.M., 2006. The functional role of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology* 51, 460–474.
- Intergovernmental Panel on Climate Change (IPCC), 2007. *Climate Change 2007. 4th Assessment Report*.
- Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8, 538–547.
- Lehsten, V., Kleyer, M., 2007. Turnover of plant trait hierarchies in simulated community assembly in response to fertility and disturbance. *Ecological Modelling* 203, 270–278.
- Lydeard, C., Cowie, R.H., Ponder, W.F., Bogan, A.E., Bouchet, P., Clark, S.A., Cummings, K.W., Frest, T.J., Gargominy, O., Herbert, D.G., Hershler, R., Perez, K.E., Roth, B., Seddon, M., Strong, E.E., Thompson, F.G., 2004. The global decline of nonmarine mollusks. *BioScience* 54, 321–330.
- Lydeard, C., Mayden, R., 1995. A diverse and endangered aquatic ecosystem of the southeast United States. *Conservation Biology* 9, 800–805.
- Lytte, D.A., Poff, N.L., 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19, 94–100.
- Master, L.M., Flack, S.R., Stein, B.A., 1998. *Rivers of Life: Critical Watersheds for Protecting Freshwater Diversity*. The Nature Conservancy, Arlington, Virginia.
- Matthews, W.J., 1998. *Patterns in Freshwater Fish Ecology*. Chapman & Hall, New York, New York.
- 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.
- Matthews, W.J., Vaughn, C.C., Gido, K.B., Marsh-Matthews, E., 2005. Southern plains rivers. In: Benke, A.C., Cushing, C.E. (Eds.), *Rivers of North America*. Elsevier, San Diego, California, pp. 283–326.
- 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.
- Mayden, R., 1985. Biogeography of Ouachita Highland fishes. *The Southwestern Naturalist* 30, 195–211.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21, 178–185.
- McMahon, R.F., Bogan, A.E., 2001. Mollusca: Bivalvia. In: Thorp, J.H., Covich, A.P. (Eds.), *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, San Diego, California, pp. 331–430.
- Merz, J.E., Moyle, P.B., 2006. Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of central California. *Ecological Applications* 16, 999–1009.
- Monroe, E.M., Newton, T.J., 2001. Seasonal variation in physiological condition of *Amblyma plicata* in the upper Mississippi River. *Journal of Shellfish Research* 20, 1167–1171.
- Moore, J.W., 2006. Animal ecosystem engineers in streams. *BioScience* 56, 237–246.
- Moore, J.W., Schindler, D.W., Carter, J.L., Fox, J., Griffiths, J., Holtgrieve, G.W., 2007. Biotic control of stream fluxes: spawning salmon derive nutrient and matter export. *Ecology* 88, 1278–1291.
- Mulholland, P.J., Best, G.R., Coutant, C.C., Hornberger, G.M., Meyer, J.L., Robinson, P.J., Stenberg, J.R., Turner, R.E., Vera-Herrera, F., Wetzel, R.G., 1997. Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf Coast of Mexico. *Hydrological Processes* 11, 949–970.
- Neves, R.J., Bogan, A.E., Williams, J.D., Ahlstedt, S.A., Hartfield, P.W., 1997. Status of aquatic mollusks in the Southeastern United States: a downward spiral of diversity. In: Benz, G.W., Collins, D.E. (Eds.), *Aquatic Fauna in Peril: The Southeastern Perspective*. Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, Georgia, pp. 43–85.
- Oklahoma Climatological Survey, 2008. *Climate Trends*. Oklahoma Climate Data Pages. Oklahoma Climatological Survey, Norman, OK.
- Oklahoma Water Resources Board (OWRB), 2000a. *Kiamichi River Basin Water Resources Development Plan*. Oklahoma City, Oklahoma.
- Oklahoma Water Resources Board (OWRB), 2000b. *Drought Indices*. Oklahoma Water News: Bimonthly Newsletter of the Oklahoma Water Resources Board July–August 2000, 1–8.
- Oklahoma Water Resources Board (OWRB), 2002. *Southeast Oklahoma Water Resources Development Plan*. Joint State/Tribal Water Compact and Water Marketing Proposals: Status Report to the Office of the Governor. Oklahoma City, Oklahoma, p. 45.
- Parmalee, P.W., Bogan, A.W., 1998. *The Freshwater Mussels of Tennessee*. Univ. Tenn. Press, Knoxville, p. 328.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change across natural systems. *Nature* 421, 37–42.
- Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16, 391–409.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestgaard, K.L., Richter, B.D., Sparks, R.E., Stomberg, J.C., 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* 47, 769–784.
- Poole, K.E., Downing, J.A., 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. *Journal of the North American Benthological Society* 23, 114–125.
- Pyron, M., Vaughn, C.C., Winston, M.R., Pigg, J., 1998. The long-term fish assemblage of the Kiamichi River, Oklahoma. *Southwestern Naturalist* 43, 45–53.
- Robison, H.W., Buchanan, T.M., 1988. *Fishes of Arkansas*. University of Arkansas Press, Fayetteville, Arkansas.
- Schindler, D.W., 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrological Processes* 11, 1043–1067.
- Schlapfer, F., Pfisterer, A.B., Schmid, B., 2005. Non-random species extinction and plant production: implications for ecosystem functioning. *Journal of Applied Ecology* 42, 13–24.
- Schroeter, S.C., Dixon, J.D., Kastendiek, J., Smith, R.O., 1993. Detecting the ecological effects of environmental impacts – a case-study of kelp forest invertebrates. *Ecological Applications* 3, 331–350.
- Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C., Firbank, L.G., 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B-Biological Sciences* 273, 2659–2665.
- Spooner, D.E., Vaughn, C.C., 2000. Impact of drought conditions on a mussel bed in the Kiamichi River, southeastern Oklahoma. *Ellipsaria Fall 2000*, 10–11.
- 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.
- Spooner, D.E., Vaughn, C.C., 2009. Species richness and thermal variation influence freshwater mussel biomass via complementarity: a partitioning approach applied to natural communities. *Ecology* 90, 781–790.
- Stenseth, N.C., Myrseth, A., Ottersen, G., Hurrell, J.W., Chan, K.S., Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297, 1292–1296.
- Strayer, D.L., 1999. Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society* 18, 74–98.
- Strayer, D.L., Downing, J.A., Haag, W.R., King, T.L., Layzer, J.B., Newton, T.J., Nichols, S.J., 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience* 54, 429–439.
- Strayer, D.L., Smith, D.R., 2003. *A Guide to Sampling Freshwater Mussel Populations*. American Fisheries Society, Bethesda, Maryland.
- Taylor, B.W., Flecker, A.S., Hall, R.O., 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* 313, 833–836.
- Townsend, C.R., 1989. The patch dynamic concept of stream community structure. *Journal of the North American Benthological Society* 8, 36–50.
- Vaughn, C.C., 2000. Changes in the mussel fauna of the Red River drainage: 1910 – present. In: Tankersley, R.A., Warmolts, D.J., Watters, G.T., Armitage, B.J., Johnson, P.D., Butler, R.S., (Eds.), *In: Proceedings of the First Freshwater Mussel Symposium*. Ohio Biological Survey, Columbus, Ohio.
- Vaughn, C.C., Gido, K.B., Spooner, D.E., 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance. *Hydrobiologia* 527, 35–47.
- Vaughn, C.C., Nichols, S.J., Spooner, D.E., 2008. Community and food web ecology of freshwater mussels. *Journal of the North American Benthological Society* 27, 409–423.
- Vaughn, C.C., Pyron, M., 1995. Population ecology of the endangered Ouachita rock-pocketbook mussel, *Arkansia wheeleri* (Bivalvia: Unionidae), in the Kiamichi River, Oklahoma. *American Malacological Bulletin* 11, 145–151.
- 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., Taylor, C.M., 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology* 13, 912–920.
- Vaughn, C.C., Taylor, C.M., Eberhard, K.J., 1997. A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys. In: Cummings, K.S., Buchanan, A.C., Mayer, C.A., Naimo, T.J., (Eds.), *Conservation and Management of Freshwater Mussels II: Initiatives for the Future*. Proceedings of a UMRCC Symposium, 16–18 October 1995, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois, pp. 157–162.
- Waller, D.L., Gutreuter, S., Rach, J.J., 1999. Behavioral responses to disturbance in freshwater mussels with implications for conservation and management. *Journal of the North American Benthological Society* 18, 381–390.
- Watters, G.T., 2000. Freshwater mussels and water quality: a review of the effects of hydrological and instream habitat alterations. *Proceedings of the First Freshwater Mollusk Conservation Society Symposium* 1999, 261–274.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Levesque, L.M.J., Vincent, W.F., 2006. Climate change effects on aquatic biota, ecosystem structure and function. *Ambio* 35, 359–369.
- Xenopoulos, M.A., Lodge, D.M., Alcamo, J., Marker, M., Schulze, K., Van Vuuren, D.P., 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology* 11, 1557–1564.
- Zavaleta, E.S., Hulvey, K.B., 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306, 1175–1177.