FINAL REPORT

Physiological determination of mussel sensitivity to water management practices in the Kiamichi River and review and summarization of literature pertaining to mussels of the Kiamichi and Little River watersheds, Oklahoma.

Submitted to:

Oklahoma Department of Wildlife Conservation
1801 N. Lincoln Blvd.
Oklahoma City, OK

By

Daniel E. Spooner
Caryn C. Vaughn, Ph.D.
Heather S. Galbraith

Oklahoma Biological Survey and Department of Zoology
111 E. Chesapeake Street
University of Oklahoma
Norman, OK 73019

FINAL REPORT

STATE: Oklahoma   **PROJECT NO:** T-10-P

PROJECT TITLE: Physiological determination of mussel sensitivity to water management practices in the Kiamichi River and review and summarization of literature pertaining to mussels of the Kiamichi and Little River watersheds, Oklahoma.

SEGMENT DATES: August 11, 2003 – September 30, 2005.

A. ABSTRACT

The freshwater mussel (Unionidae) fauna of North America is the most diverse in the world, but is highly threatened, with major declines of mussel populations and species diversity occurring over the past century. Based on archeological evidence, the overall mussel species composition of southeastern Oklahoma rivers has changed little over the last several thousand years. While few rivers in the region have lost species outright, within rivers both the number of sites at which species occur and species abundances have declined. Nonetheless, the four rivers of far southeastern Oklahoma (Kiamichi, Little, Glover and Mountain Fork) continue to harbor a rich and overall healthy mussel fauna. There are approximately 52 extant unionid mussel species known to presently occur in Oklahoma waters, and 41 of these (80%) occur in these rivers, including three federally endangered species, the Ouachita rock pocketbook, the winged mapleleaf, and the scaleshell.

The major cause of mussel decline in the U.S. is from the alteration of the natural flow regime of rivers. Because mussels are dependent on fish hosts, any effects of hydrologic alterations on fish hosts also impacts mussel populations. Mussels evolved in rivers that typically experienced seasonal periods of low and high flow. Recent studies indicate that instream flow needs are not the same for all mussel species, and that natural, temporal variability in flows is important to maintaining diverse mussel assemblages.

This study combined comparative field observations with laboratory-derived empirical measurements to address the following three questions: *(1) What is the best method for predicting the actual water temperatures experienced by mussel populations?; (2) What is the physiological response of freshwater mussels to a variety of water temperatures?; and (3) Can we predict the physiological responses, and thus stress levels, experienced by mussels in streams?* We used stepwise linear regression to create models predicting ambient water temperature (i.e. water temperatures actually experienced by the mussels) for sites in the Kiamichi River using field-collected data on air and water temperatures, and discharge. We performed laboratory experiments and made comparative field observations on mussel species commonly found in the Kiamichi River to determine species differential susceptibility to thermal stress. Laboratory estimates of thermal response were compared to field estimates to corroborate our findings and ensure that results were applicable to natural streams.   For each field site, we estimated the

proportion of the mussel community experiencing low or high stress depending on ambient water temperature along a gradient from 24 to 44°C. We did this using data on mussel abundance and community composition at field sites combined with our predictive temperature model and laboratory results of species differential responses to thermal stress.

This study demonstrates that mussel populations can experience significant stress prior to the onset of mortality. In addition, we may be able to predict when mussels may be most susceptible to impacts. We found that mussels experience species-specific, sub-lethal stress when exposed to high water temperatures (generally greater than 35°C, but lower for some species such as *A. ligamentina*). These high water temperatures occur in southeastern Oklahoma rivers during the summer months when low discharge leads to the formation of isolated pools. These high water temperatures lead to mussel stress and may lead to death, either directly from thermal shock or indirectly from oxygen deprivation as the results of associated algal blooms. In the absence of flow, mussels with lower thermal thresholds will suffer the highest stress and mortality, and thus overall effects will depend on the species composition of a particular mussel bed. We recommend using *Actinonaias ligamentina* as an indicator species for the health of mussel beds in the Kiamichi river. *A. ligamentina* was the most thermally sensitive mussel in our study and is common throughout the Kiamichi River. By managing to protect *A. ligamentina*, we should be able to protect the majority of mussel species in the river including the federally endangered species, *A. wheeleri* and *L. leptodon*, which co-occur with *A. ligamentina*. We recommend using the average temperature-stream relationship and predictive figures outlined by this project to monitor potential temperatures experienced by mussels and to increase stream flows to prevent the formation of isolated pools during periods of high air temperature.

Part I. Physiological determination of mussel sensitivity to water management practices in the Kiamichi River.

B. OBJECTIVES

The purpose of this study was to determine the most effective metric of physiological condition for predicting if mussel populations are stressed *prior to* the occurrence of mortality events. We combined comparative field observations with laboratory-derived empirical measurements to address the following three questions:

> *(1) What is the best method for predicting the actual water temperatures experienced by mussel populations?*
>
> *(2) What is the physiological response of freshwater mussels to a variety of water temperatures?*
>
> *(3) Can we predict the physiological responses, and thus stress levels, experienced by mussels in streams?*

C. NEED

Freshwater ecosystems are globally imperiled as a result of reduced water quality and altered flow regimes associated with increased human demands. Streams and rivers are an important intermediary of nutrient and energy flow between aquatic, marine and terrestrial ecosystems (Allan & Flecker 1993). Anthropogenic disturbances including river channelization, impoundments, and water diversion threaten to alter natural flow regimes and the balance of energy flow between ecosystems (Allan *et al.* 1997; Cote & Jelnikar 1999) and have resulted in an overall decline in water quality and ecosystem stability. Urban sprawl associated with population growth magnifies the problem by increasing the demand for water and, thus, increasing the amount of river regulation required to meet those needs (Richter et al. 1997). Further, drought events associated with high air temperature and reduced precipitation exacerbate the problem by elevating stream temperatures beyond biologically stable conditions (Layzer & Madison 1995; Golladay *et al.* 2004). Proper management of freshwater resources requires balancing human consumption of water with the biological needs of freshwater fauna.

Freshwater mussels are a good model system to examine the effects of flow and temperature regime change. Freshwater mussels can represent a dominant fraction of the aquatic biomass and provide important ecological services to streams including water column filtration and nutrient recycling (Vaughn & Hakenkamp 2001). In addition, mussels act as an energy conduit transferring materials from the water column to the streambed sediment, facilitating other organisms (Vaughn et al. 2004). Like many other invertebrates, mussels are thermo-conformers, meaning that they passively adjust their metabolic thermostat to match the surrounding environmental temperature (Williams & McMahon 1985; McMahon & Bogan 2001). This relationship has significant implications for both the physiological health of the mussels and the subsequent ecological services they provide to streams.

Mussels use a variety of approaches to combat the effects reduced flow and increased water temperatures, each with their own benefits and costs. In the event of dewatering, mussels may move to deeper, cooler water (Chen 1998). This strategy is costly, however, as coarse substrate and distance to cooler refugia may limit burrowing capacity and prove energetically unfeasible. Mussels also may exhibit 'mantle edge behavior', a practice in which a mussel gapes passively allowing oxygen to diffuse across the mantle tissue (Byrne 1998; Chen 1998). Mussels that exhibit mantle edge behavior survive by meeting the minimum requirements for aerobic respiration. Consequently, water loss across the mantle limits the duration for which this strategy is effective (McMahon 1979). An alternative strategy is to close the valves and anaerobically catabolyze stored energy reserves. This strategy is highly dependent upon both the amount of available stored energy and the duration of dewatering (Chen 1998). Depending upon the energy source being catabolyzed, toxic by products, including ammonia, may preclude the effectiveness of stored energy catabolism over long periods (Byrne 1998).

Southeastern Oklahoma is a center of aquatic biodiversity with 101 fish and 41 mussel species (Vaughn *et al.* 1996; Vaughn 2000) and no documented mussel extirpations

3

(Vaughn et al. 1996). Three federally endangered species occur in these rivers, the Ouachita rock pocketbook (*Arkansia wheeleri*), the winged mapleleaf (*Quadrula fragosa*), and the scaleshell (*Leptodea leptodon*).   In recent years, southeastern Oklahoma streams have been exposed to drought conditions resulting in lower flow and increased water temperature. This phenomenon has been exacerbated by the practice of holding water in upstream reservoirs, which further reduces downstream water volume and flow and increases temperatures, and can have devastating effects on mussel populations. For example, in the summer of 2000 there was a record drought in this area. By the end of August, large stretches of the Kiamichi River had become a series of pools isolated by long reaches of dry riverbed. Elevated water temperature and desiccation associated with emersion contributed to high mussel mortality (Figure 1) (Spooner & Vaughn 2000). Mussels that survived the drought event were larger, and often found in deeper cooler water (Figure 1).

Water volume, current velocity, and temperature are all inter-related and important to the well-being and survival of mussel communities (see literature review in Part II, below), Given the projected demands for water use in southeastern Oklahoma (i.e. water transfers to Texas, reservoirs etc…) it is imperative that we develop a protocol for determining the sensitivity of mussels to reduced water flows and subsequent increased temperature prior to the onset of mortality events. If we can predict, from flow and temperature data, when mussel populations are stressed, we should be able to manage water resources to protect mussels from mortality events. This study examines the relationship between stream-flow and thermal refugia for freshwater mussel populations.

D. APPROACH

(1) What is the best method for predicting the actual water temperatures experienced by mussel populations?

We used stepwise linear regression to create models predicting ambient water temperature (i.e. water temperatures actually experienced by the mussels) for each site using stepwise linear regression and field-collected data on air and water temperatures, and discharge.

(2) What is the physiological response of freshwater mussels to a variety of water temperatures?

We performed laboratory experiments and made comparative field observations on mussel species commonly found in the Kiamichi River to determine species differential susceptibility to thermal stress. Laboratory estimates of thermal response were compared to field estimates to corroborate our findings and ensure that results were applicable to natural streams.

(3) Can we predict the physiological responses, and thus stress levels, experienced by mussels in streams?

For each field site, we estimated the proportion of the mussel community experiencing low or high stress depending on ambient water temperature along a gradient from 24 to 44°C. We did this using data on mussel abundance and community composition at field sites combined with our predictive temperature model and laboratory results of species differential responses to thermal stress.

E. RESULTS AND DISCUSSION

(1) What is the best method for predicting the actual water temperatures experienced by mussel populations?

We created models to predict ambient water temperature (i.e. water temperatures actually experienced by the mussels) for each site using stepwise linear regression and the following predictor variables: discharge, maximum air temperature (atmax), minimum air temperature (atmin), average air temperature (atav), heating degree days (HDD) and cooling degree days (CDD). Correlation analysis indicated that all predictor variables excluding atav and discharge were collinear and described overlapping variation. We then performed regression analysis with atav and discharge values for each site to predict ambient stream temperature (Table 2).

Using our derived models, water temperature for sites along the Kiamichi River (Figure 2) can be predicted from air temperature as follows:

Site $_{(A)}$ water temp (°C) = 6.062+0.408(atavClayton °C) + 0.013(atavClayton °C)^2

Site $_{(B, C, D)}$ water temp (°C) = 5.991+0.0576(atavClayton °C) + 0.009(atavClayton °C)^2

Site $_{(E, F, G, H)}$ water temp (°C) = 6.277+0.260(atavAntlers °C) + 0.019(atavAntlers °C)^2

(2) What is the physiological response of freshwater mussels to a variety of water temperatures?

We performed laboratory experiments and made comparative field observations on mussel species commonly found in the Kiamichi River to determine species differential susceptibility to thermal stress. Laboratory estimates of thermal response were compared to field estimates to corroborate our findings and ensure that results were applicable to natural streams.

(2a) Laboratory studies

Mussel respiration rates, tissue glycogen concentration, and body condition index (BCI) represent three different temporal scales for which observed effects of temperature on mussel physiology may be quantified. Respiration rates represent relatively small

temporal scale effects of temperature, whereas glycogen and BCI represent the integration of growth and energy over a seasonal or longer time frame.

Using respirometers (respiration chambers) in temperature-controlled environmental chambers, we quantified respiration rates, tissue glycogen concentration, and BCI as surrogate measures of physiological condition for eight species of mussels (Table 3). Mussels were collected from the Little River in late October 2004 and acclimated to four temperatures ($5^{o}C$, $15^{o}C$, $25^{o}C$, $35^{o}C$) for a period of two weeks at the University of Oklahoma Aquatic Research Facility (ARF). Mussels then were placed in respirometers containing filtered pond water for one hour at their respective acclimation temperature. Respiration rates were calculated as the change in oxygen concentration over one hour, standardized for body size and chamber volume. Oxygen concentration was determined using a calibrated Orion 850A polarized probe. Upon completion of a respiration experiment, mantle tissue (~30 mg) was collected from each mussel and stored at $-80^{o}C$ for glycogen determination (Berg et al. 1995). Glycogen concentration was quantified colorimetrically using the Phenol-Sulphate method and compared to glycogen reference material (Naimo et al. 1998). Body condition index (BCI) was calculated as the total mussel wet mass divided by the shell length. The effect of temperature on respiration rate was modeled for each species using polynomial regression.

Acclimation temperature significantly influenced the condition of mussels and suggested a threshold of thermal stress above $30^{o}C$. The response to temperature was species-specific, with strongest effects of temperature on *Actinonaias Ligamentina* (Figure 3). All mussel species exhibited signs of thermal stress; however, mortality during acclimation was limited to *A. ligamentina* at temperatures above $35^{o}C$. Although glycogen and BCI exhibited similar response trajectories, they were not predictive and displayed high variation in response to temperature treatments. However, glycogen concentration was significantly lower at $35^{o}C$ for *O. reflexa* (figure 4), *F. flava* (figure 5), and *A. ligamentina*. *Actinonaias ligamentina* was the only mussel with a significant decline in body condition index with respect to temperature.

Temperature treatments significantly influenced mussel respiration in a highly predictive, species-specific manner (Table 4). Respiration rates of *A. ligamentina* (Figure 3), *L. cardium* (Figure 6), and *T. truncata* (Figure 7) declined above $32^{o}C$, implying some form of thermal inhibition. Upon extrapolating the relationship to 39-42°C, respiration rates declined to zero implying a larger, more severe response to thermal stress. In addition, we observed *A. ligamentina* and *T. truncata* mortality throughout the acclimation process, supporting the conclusion that a temperature range of 35 to 42°C encroaches on the critical thermal maxima for these species. *Megalonaias nervosa* (Figure 8), *A. plicata* (Figure 9), *O. reflexa* (Figure 4), *F. flava* (Figure 5), and *Q. pustulosa* (Figure 10) respiration responded in a predictable fashion; however, the relationship degraded beyond $35^{o}C$ suggesting that these mussels may not undergo as much stress until higher temperatures are experienced. More data points are required beyond $35^{o}C$ to increase the resolution and determine potential critical thermal maxima points.

(2b) Field observations

The objectives of the comparative field surveys were to observe the natural variation in mussel condition and stream temperature, and ground truth our empirically-determined physiological models. Further, we wanted to determine if the condition of mussels differed above or below the confluence of Jackfork Creek, a tributary of the Kiamichi River. Surveys were conducted in two separate blocks. The first block encompassed a seasonal collection of mussel tissue across four sites in the Kiamichi River throughout 2003-2004. A second block of field surveys was conducted in the summer of 2005 across seven sites to improve the quality of the physiological models and increase the breadth of river for monitoring.

(2b*i*) Block 1 field collection (summer 2003-spring 2004)

We sampled four mussel beds (sites A, B, C, and E) during the summer (August 2003), fall (November 2003), winter (January 2004), and spring (May 2004). At each site, we quantified water temperature, water depth and discharge. We conducted times searches (minimum of two hours) in each mussel bed and collected individuals of at least four species of mussel. For each individual mussel we recorded length, wet mass, and collected a 30 mg mantle tissue sample. Tissue samples were placed in liquid nitrogen and stored at -80°C until analysis. Our ability to sample sufficient numbers of mussels at field sites varied across seasons, inhibiting our ability to standardize the numbers and species types collected for analyses.

Glycogen concentrations were determined with the methods outlined for the laboratory experiments above. Two-way analysis of variance (ANOVA) was used to compare glycogen concentrations of different species across seasons (summer, fall, winter, and spring), sites (A, B, C, and E), and above and below the confluence of the river with Jackfork Creek. Although glycogen was collected and quantified for multiple species over a variety of sampling periods, statistical assumptions (orthogonality and sample size) were met only for the analysis of two species, *A. ligamentina* and *A. plicata*. Therefore, we also pooled glycogen data across all collected species and performed the same ANOVA as above. Sites and seasons were compared using post-hoc multiple comparison procedures with a Bonferonni adjustment for alpha.

Tissue glycogen concentration was highly variable across sites and seasons. Glycogen concentration appeared to be lowest and least variable at site E across seasons for both *A. ligamentina* and *A. plicata* (Figure 11). Glycogen appeared to be lowest in the summer, increased in the fall and winter, and then declined in the spring. This relationship was only significant for *A. plicata*, although the same trend was apparent for *A. ligamentina*. *Amblema plicata* glycogen was significantly higher at the sites located above the confluence of Jackfork Creek in the fall and winter (Figure 12). Despite a non-significant main-effects result, post-hoc comparisons determined that *A. ligamentina* tissue glycogen content was highest above the confluence of Jackfork Creek in the winter. Although not significant, there was an overall trend of higher glycogen concentrations above Jackfork Creek in the spring and summer.

7

Pooled species also had the lowest and least variable glycogen concentrations for site E, while highest concentrations were observed for site B (Figure 13). A seasonal trend of glycogen increasing from summer to winter and then declining in spring was observed at sites A and C. Mussels located at sites below the confluence of Jackfork Creek had the lowest and least variable concentrations of glycogen (Figure 13).

Field-collected glycogen data suggest that, despite high variation, mussels appear to be in better condition above the confluence of Jackfork Creek. However, mean water temperatures above and below the confluence were not significantly different. 2003-2004 was relatively mild with water temperatures only reaching a high of 33°C. Although we were able to detect significant differences between sites, the glycogen data collected were not very predictive. To adequately predict mussel stress, alternative physiological parameters including respiration are required.

(2b*ii*) Block 2 field collection (summer 2005)

In the summer of 2005 southeastern Oklahoma experienced an extended period of low precipitation, low discharge, and high air and water temperatures, i.e. a drought. Because rainfall and temperature were moderate during the 2003-04 sampling period, we decided to extend our sampling to encompass these drought conditions. Because our previous work had shown that respiration rates were highly predictive of mussel physiological condition, but that glycogen was not, we concentrated our efforts on obtaining field measurements of mussel respiration rates. In addition, we increased the number of sampling sites to seven (sites A, C, D, E, F, G, and H) (Figure 2).

At each site we performed timed searches and excavated quadrats (n=15) to estimate species abundance (Vaughn et al. 1997). We selected five individuals from each of four species (*A. ligamentina*, *A. plicata*, *Q. pustulosa*, and *F. flava*) and gently scrubbed them to remove biofilm. Mussels were then placed into individual containers containing 500 ml of filtered (precombusted GFF filters) river water. Oxygen concentration was measured using a calibrated Orion 850A polarized probe, and each container was placed back into the river to maintain ambient environmental temperatures. After 1 hour, the containers were collected and final dissolved oxygen concentration quantified. We measured length and mass of each mussel and returned them to the streambed. Water temperatures were measured with a digital temperature probe. Mussel respiration was calculated as the change in dissolved oxygen concentration over one hour relative to body size (cm) and container volume. Polynomial regression was performed comparing respiration rates to stream temperature (Table 5).

Overall, estimates of respiration rates obtained in the field were higher than those quantified in the laboratory. This phenomenon is well documented across taxa, as organisms tend to be less stressed under natural field conditions than under laboratory conditions (Schmidt-Nielson 1998). Nevertheless, laboratory and field-derived respiratory responses to temperature were similar for most species. *Actinonaias ligamentina* respiration declined at 32°C and approached zero at 38°C, verifying our

empirically derived estimate of thermal stress (Figure 14). *Amblema plicata* respiration declined at 35°C and approached zero at 42°C suggesting that this species has higher thermal tolerance than *A. ligamentina* (Figure 14). Further, these findings were consistent with the laboratory data as the decline in respiration occurs beyond the 35°C limit. *Quadrula pustulosa* and *Fusconaia flava* responded to temperature similarly as their respiration declined 34-35°C and both approached zero at 38-39°C (Figure 15). These data also are consistent with the laboratory data, as both species declined after the 35°C limit.

(3) Can we predict the physiological responses, and thus stress levels, experienced by mussels in streams?

Combined species performance data from the laboratory and field studies demonstrate that *A. ligamentina*, *L. cardium*, and *T. truncata* experience some form of stress at 32°C, and to a greater extent at 38°C. These results are corroborated by laboratory observations of significant mortality of these species while acclimating at 35°C. *Fusconaia flava*, *Q. pustulosa*, and *A. plicata* are more tolerant of warm temperatures, but begin to exhibit stress at 34-35°C; however, *Q. pustulosa* and *F. flava* differ from *A. plicata* in that exhibit maximal stress at 38°C, while *A. plicata* exhibits maximal stress at 42°C. Unfortunately, data above 35°C were not available to estimate the upper thermal stress of *M. nervosa* and *O. reflexa*.

Although only six of the eight species examined could be used to estimate mussel condition, these six species encompass over 80% of the mussel biomass in the Kiamichi River (Spooner & Vaughn, unpublished). Because we can precisely predict the physiological response of these mussels to temperature stress, and because these mussels comprise the majority of the mussel community, we can use this knowledge to estimate how low water levels combined with high water temperatures impact entire mussel beds. We did this using mussel abundance data collected in 2005, predictions from our species-specific physiological performance models, and field measures of water temperature and mussel condition. We used abundance data to estimate the relative biomass of different mussel species for our eight study sites. Based on the results of our physiology models (Figures 3 – 10), we defined 'low stress' as mussels with declining respiration rates and 'high stress' as mussels whose respiration rate approached zero (i.e. they stopped respiring). Then, for each site, we estimated the proportion of the mussel community experiencing low or high stress depending on ambient water temperature along a gradient from 24 to 44°C. Figure 16 illustrates the proportion of the mussel community experiencing low stress (dark shade, decline in respiration rate) and high stress (light shade, respiration rates approach zero) for the eight sites. For example, site A contains a high proportion of thermally-tolerant species (*A. plicata*) and a lower proportion of thermally sensitive species (*A. ligamentina*); thus, mussels at this site do not exhibit stress until temperatures of around 35°C. In contrast, site C contains a higher proportion of thermally sensitive mussels (*A. ligamentina* and *L. cardium*), and thus the mussel bed as a whole is more susceptible to thermal stress.

Our results demonstrate that, within the region of southeastern Oklahoma covered by this study, we can predict the proportion of a mussel community that will be impacted summer low flows if we know the species composition of the mussel bed and the ambient water temperature. Gathering water temperature data is costly and time consuming; however, the model we developed (Question 1, above) demonstrates that we can accurately predict water temperature from air temperature, which is readily available to managers.

CONCLUSIONS AND RECOMMENDATIONS

1. Mussel populations are impacted before mortality occurs.

Traditionally, mussel populations have been assumed to be unimpacted until mortality events occur. This study demonstrates that mussel populations can experience significant stress prior to the onset of mortality. In addition, we may be able to predict when mussels may be most susceptible to impacts. For example, field-collected glycogen data demonstrate that mussel condition increases from summer to winter and declines in the spring. This pattern is likely due to seasonal, energetic investment in reproduction. Reproduction commonly occurs in the spring-summer seasons (Bauer 1998; Parmalee & Bogan 1998) and mussels typically catabolize glycogen reserves during gametogenesis and re-supply their glycogen stores following gamete release (Chen 1998; Baker & Hornbach 2001). Thus effects of events that cause mussels to catabolyze glycogen, such as thermal stress, will be magnified during periods of reproduction. We can use this kind of information to manage mussel populations, protect them from massive mortality events, and hopefully ensure adequate future reproduction.

2. High water temperatures are stressful to mussels. Effects of high water temperatures can be ameliorated by managing stream flow.

Our results demonstrate that mussels experience species-specific, sublethal stress when exposed to high water temperatures (generally greater than 35°C, but lower for some species such as *A. ligamentina*). These high water temperatures occur in southeastern Oklahoma rivers during the summer months (Figure 17) when low discharge leads to the formation of isolated pools. Without the cooling, flushing effect of river flows, ambient water temperatures rise rapidly, and we have measured temperatures exceeding 40°C in such stagnant pools in both the Kiamichi and Little rivers (Figure 18). These high water temperatures lead to mussel stress and eventual death, as described above. In addition, impacts of such mussel mortality can rapidly accelerate because nutrients released by decaying mussel flesh can lead to algal blooms, subsequent oxygen depletion in the stagnant pools, and large increases in toxic ammonia concentrations. Although mussels are typically tolerant of low dissolved oxygen levels, the combination of low oxygen, high ammonia, and high temperatures are often lethal (Spooner & Galbraith, unpublished data(Cope et al. 2003)). Adequate stream flows can prevent this by lowering ambient water temperatures and by flushing decaying mussel flesh and nutrients from the system. We recommend using the average temperature-stream relationship and predictive figures outlined by this project to monitor potential temperatures experienced by mussels and to increase stream flows to prevent the formation of isolated pools during periods of high air temperature.

3. Current water management practices appear to be impacting mussel health:
Glycogen concentrations were generally higher above the confluence of the Kiamichi river with Jackfork Creek, suggesting that mussels may potentially be impacted by water management practices. The mechanism for this relationship is unclear and these results should be interpreted cautiously as they are based on a small sample size (we did not have very many sites above Jackfork Creek). In addition, our field glycogen samples were collected during a relatively mild year (2003-2004); under severe drought conditions, such as the summer of 2000, effects of holding water in Sardis Reservoir, further decreasing flows and increasing water temperatures in lower sections of the river, may be more severe. This observation is supported by our laboratory data showing that mussel physiological stress increases with water temperature.

4. River flows should be managed to protect the most susceptible species.
In the absence of flow, mussels with lower thermal thresholds will suffer the highest stress and mortality, and thus overall effects will depend on the species composition of a particular mussel bed.   We recommend using *A. ligamentina* as an indicator species for the health of mussel beds in the Kiamichi river. *Actinonaias ligamentina* was the most thermally sensitive mussel in our study and is common throughout the Kiamichi River. By managing to protect *A. ligamentina*, we should be able to protect the majority of mussel species in the river including the federally endangered species, *A. wheeleri* and *L. leptodon*, which co-occur with *A. ligamentina.*

F. SIGNIFICANT DEVIATIONS

In the summer of 2005 southeastern Oklahoma experienced an extended period of low precipitation, low discharge, and high air and water temperatures, i.e. a drought. Because rainfall and temperature were moderate during the 2003-04 sampling period, we decided to extend our sampling to encompass these drought conditions. Because our previous work had shown that respiration rates were highly predictive of mussel physiological condition, but that glycogen was not, we concentrated our efforts on obtaining field measurements of mussel respiration rates. In addition, we increased the number of sampling sites to from four to seven, to improve the quality of the physiological models and increase the breadth of river for monitoring.
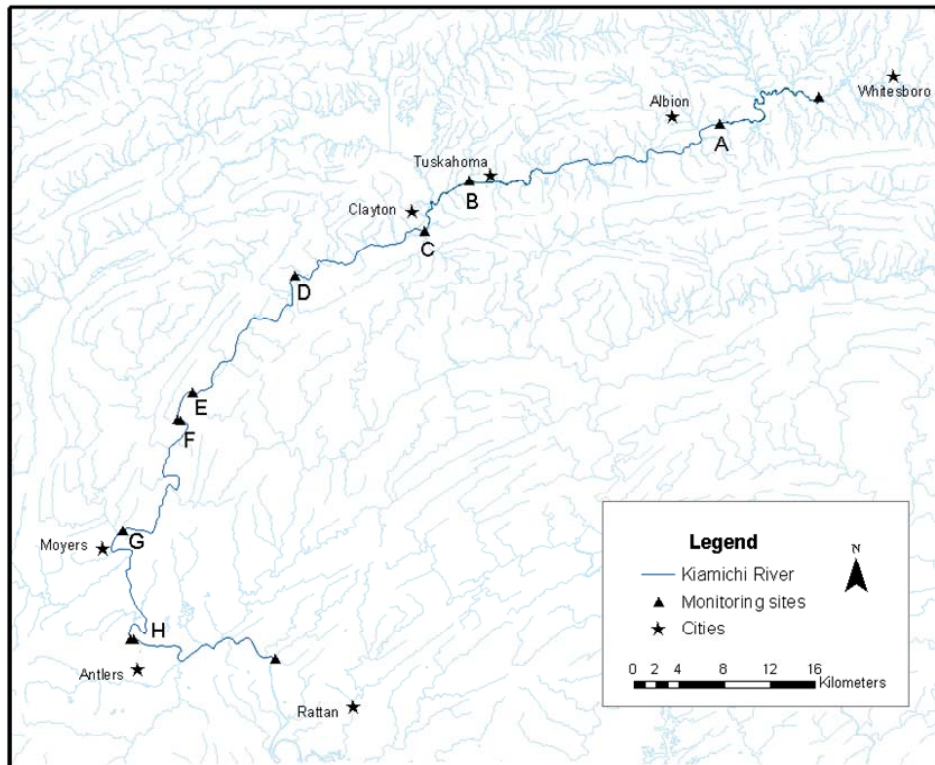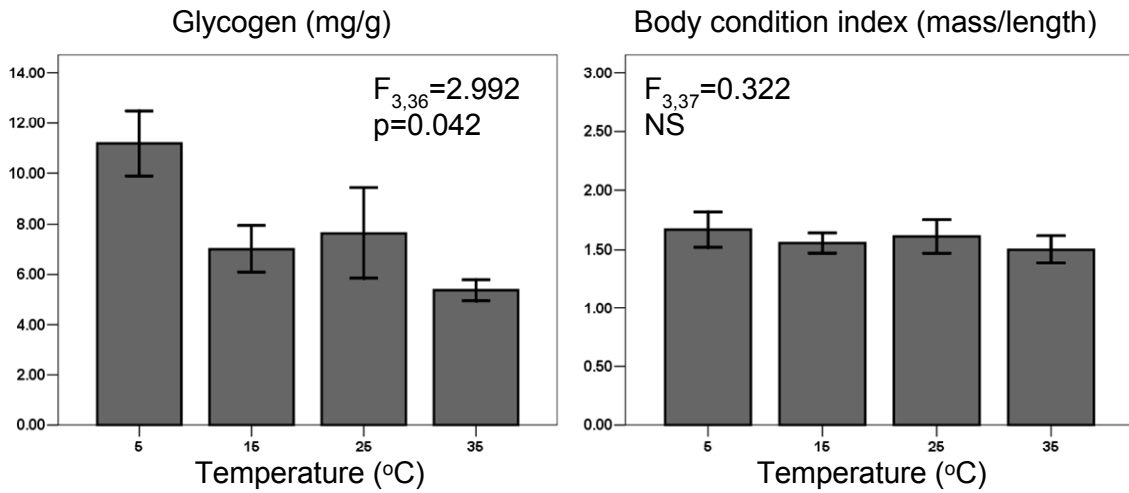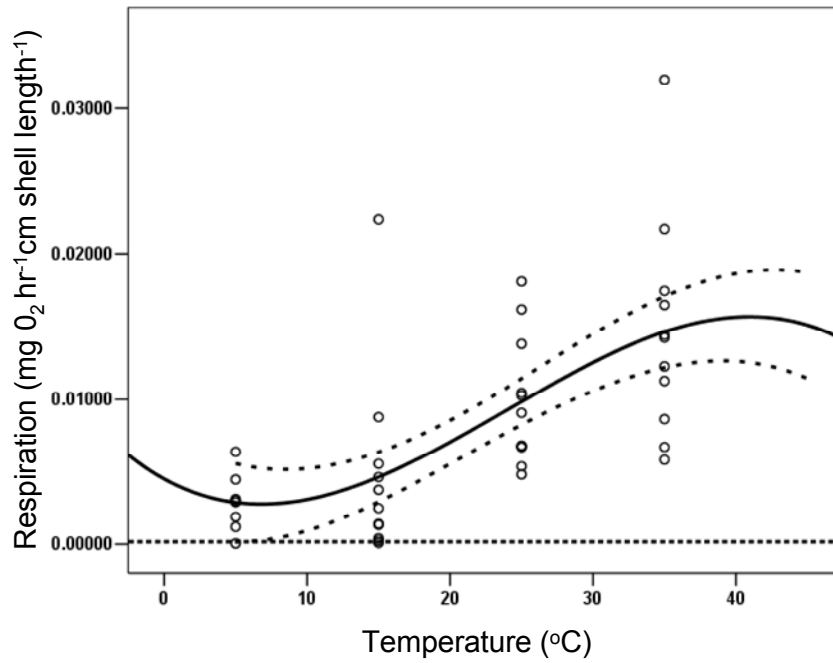
Figure 2. Map of field sites located along the Kiamichi River.
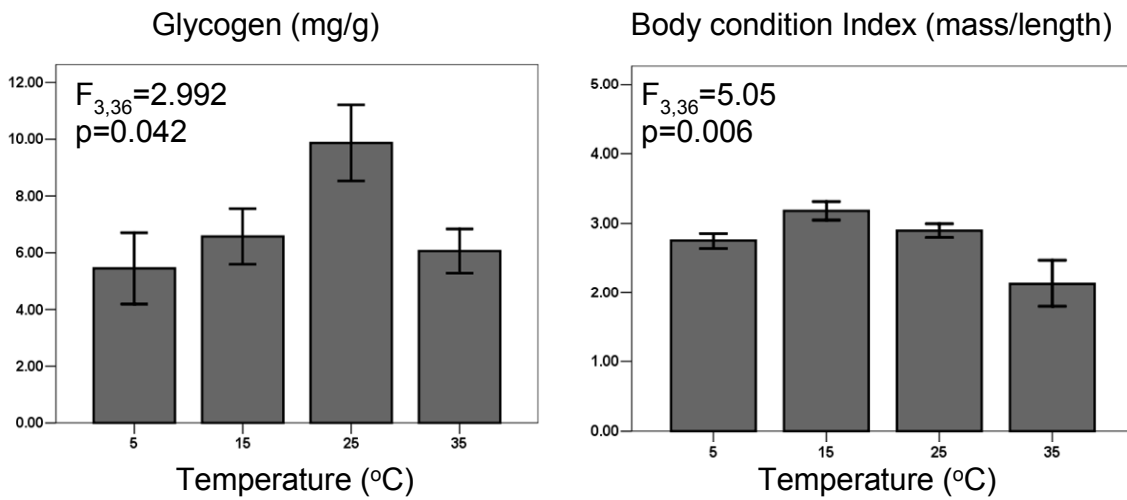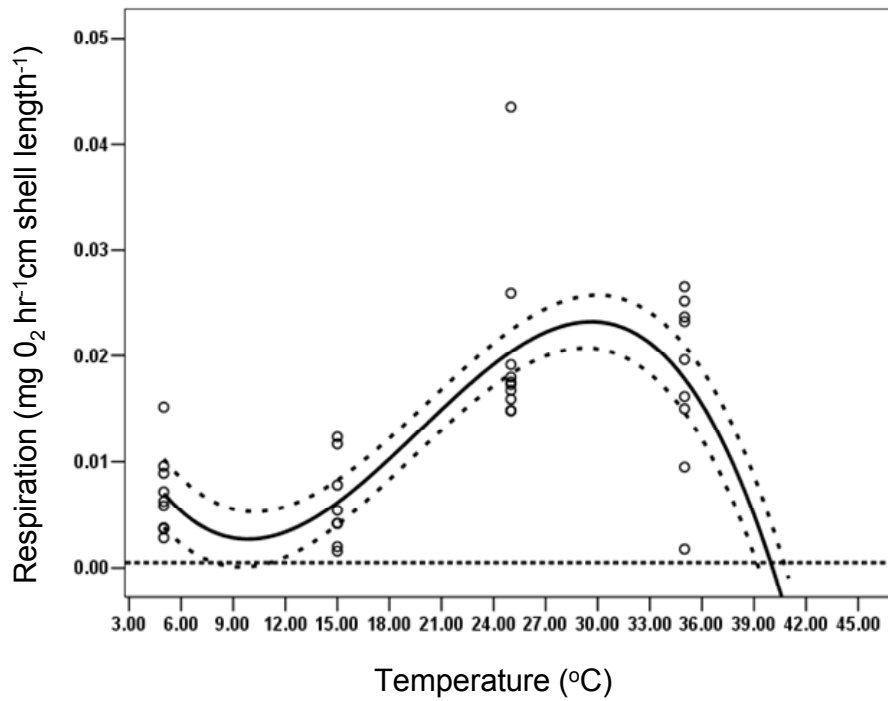
Figure 3. Physiological response of *A. ligamentina* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.
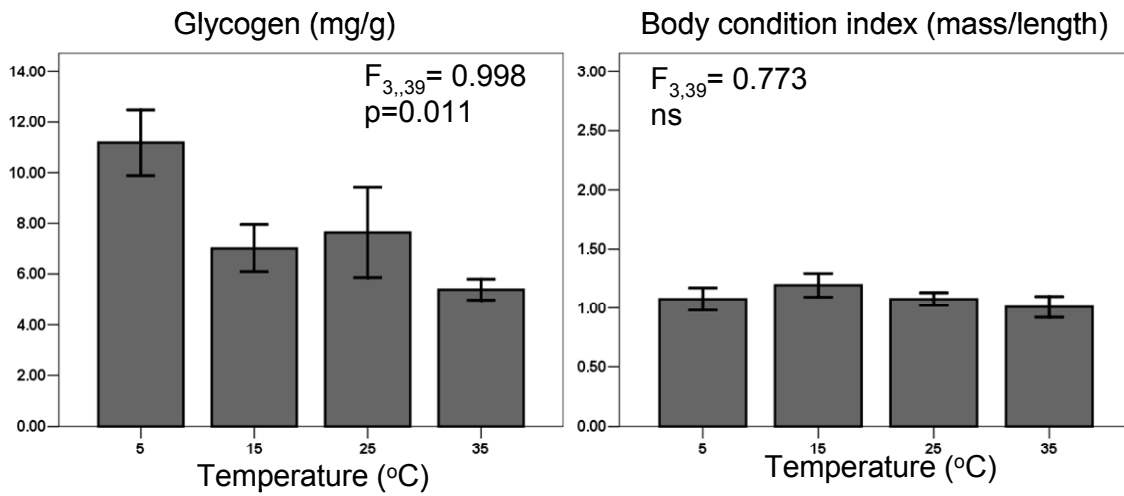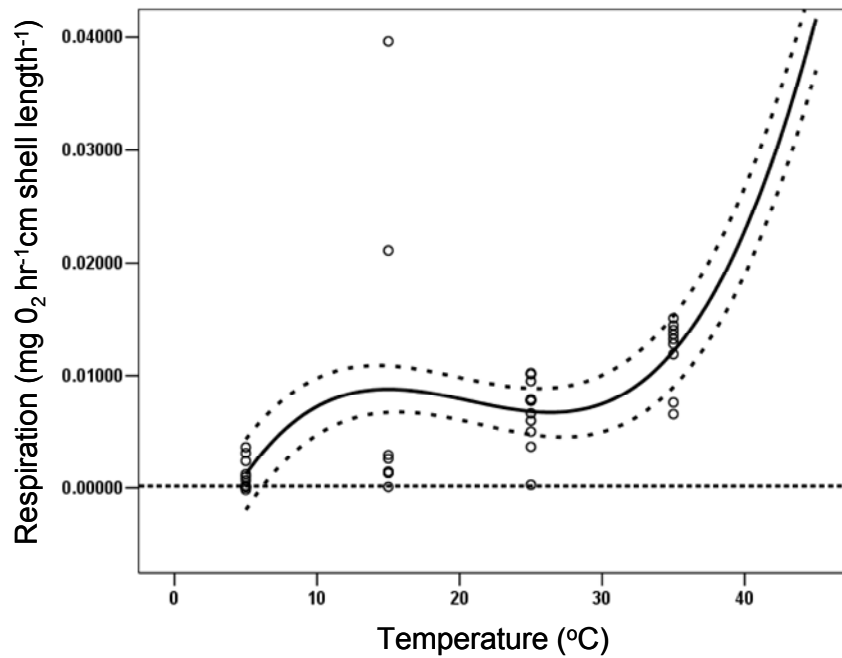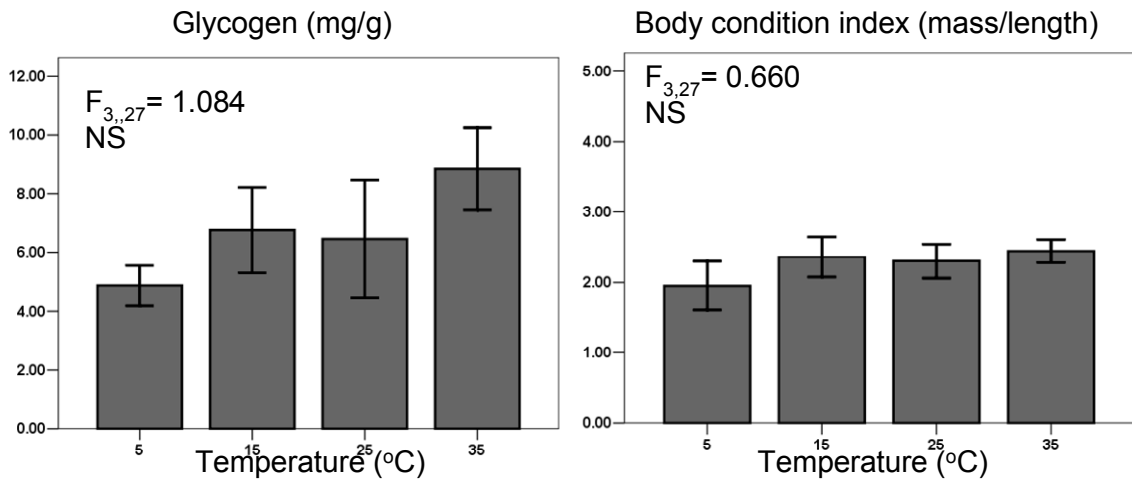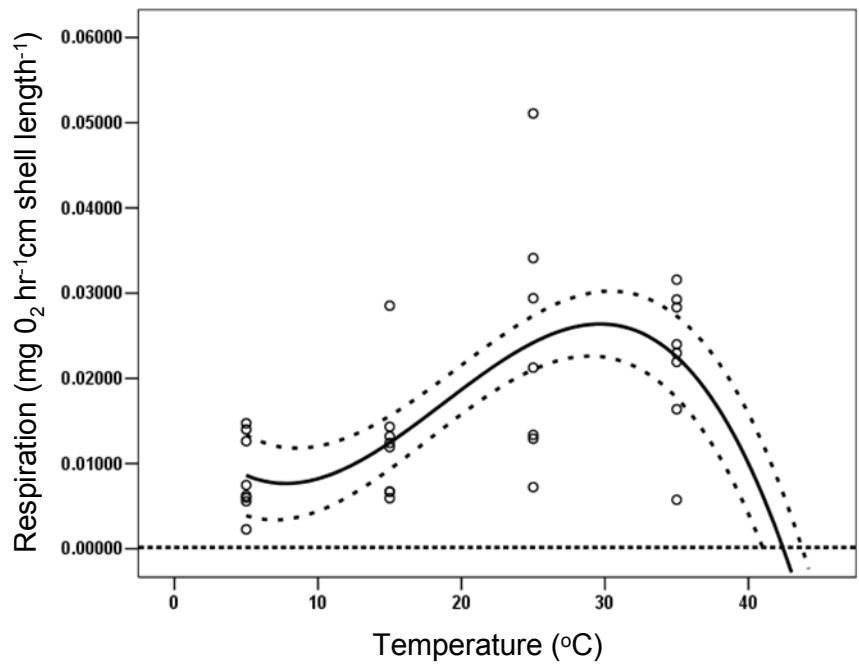
Figure 4. Physiological response of *O. reflexa* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.
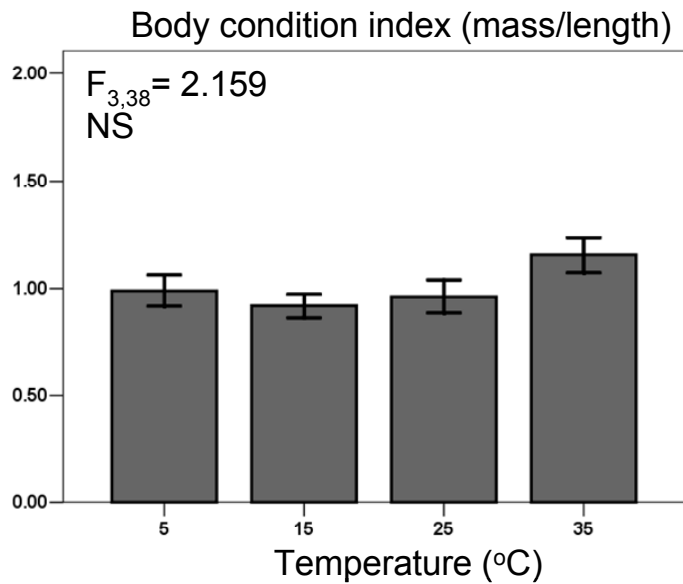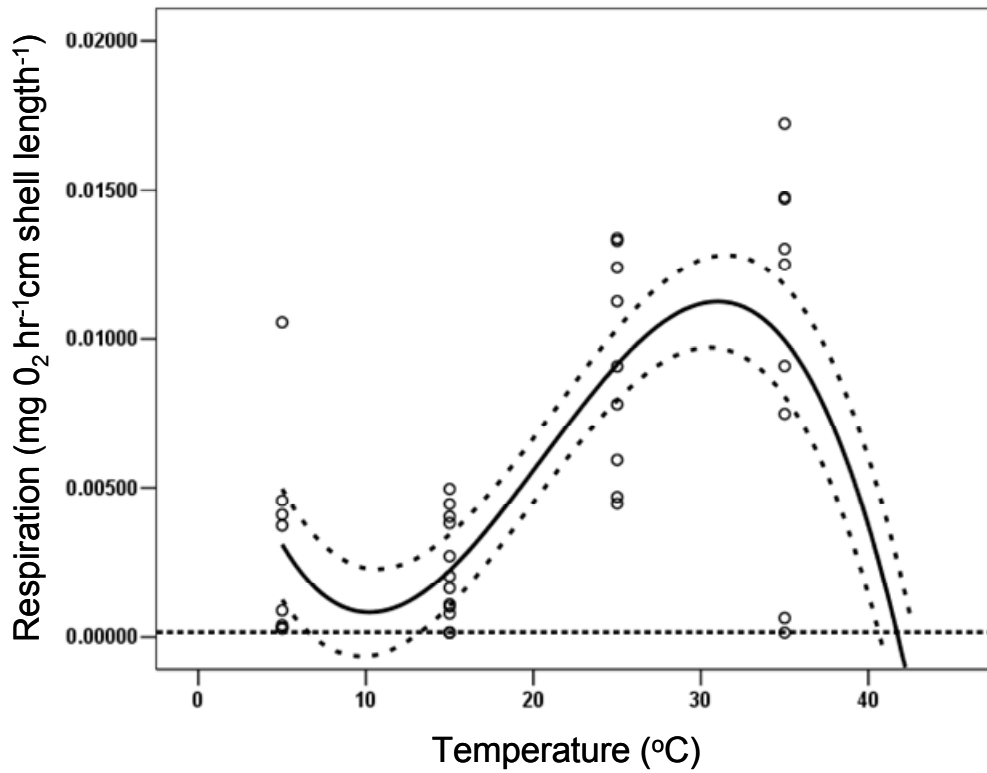
Figure 5. Physiological response of *F. flava* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.

Figure 6. Physiological response of *L. cardium* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.

Figure 7. Physiological response of *T. truncata* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.
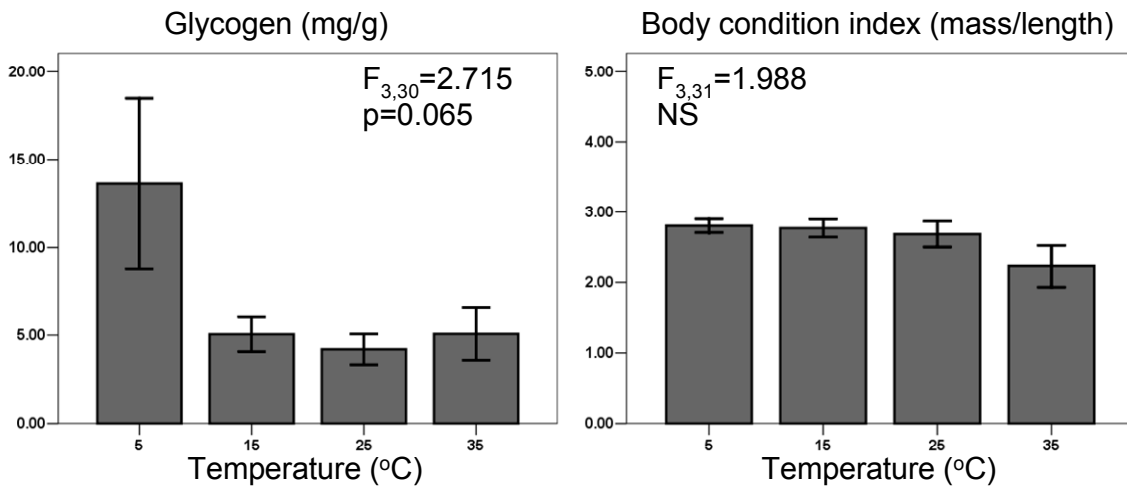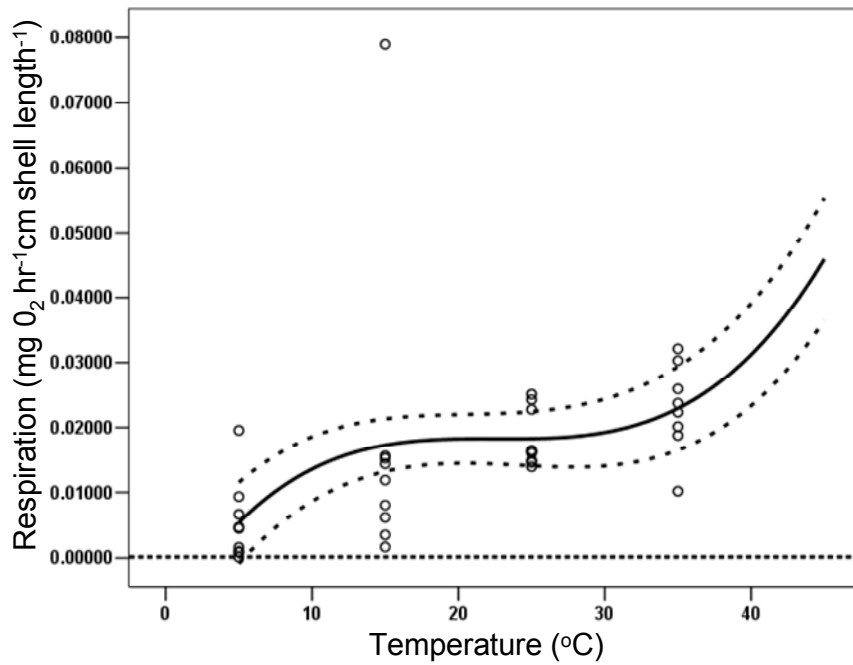
Figure 8. Physiological response of *M. nervosa* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.
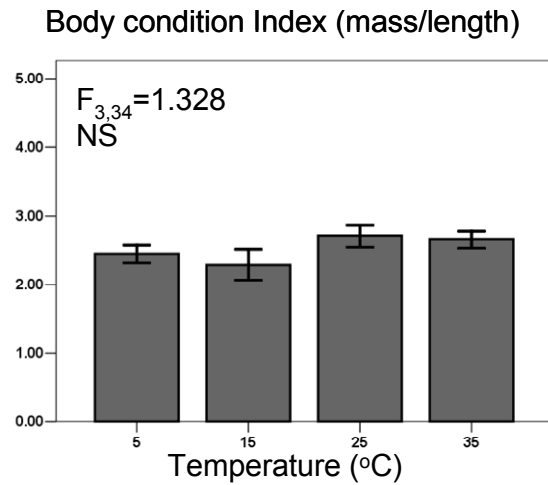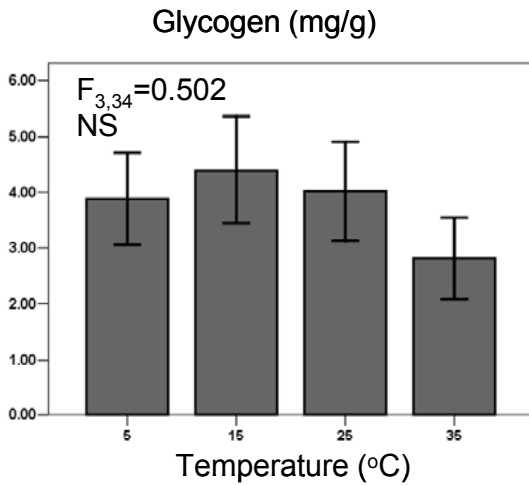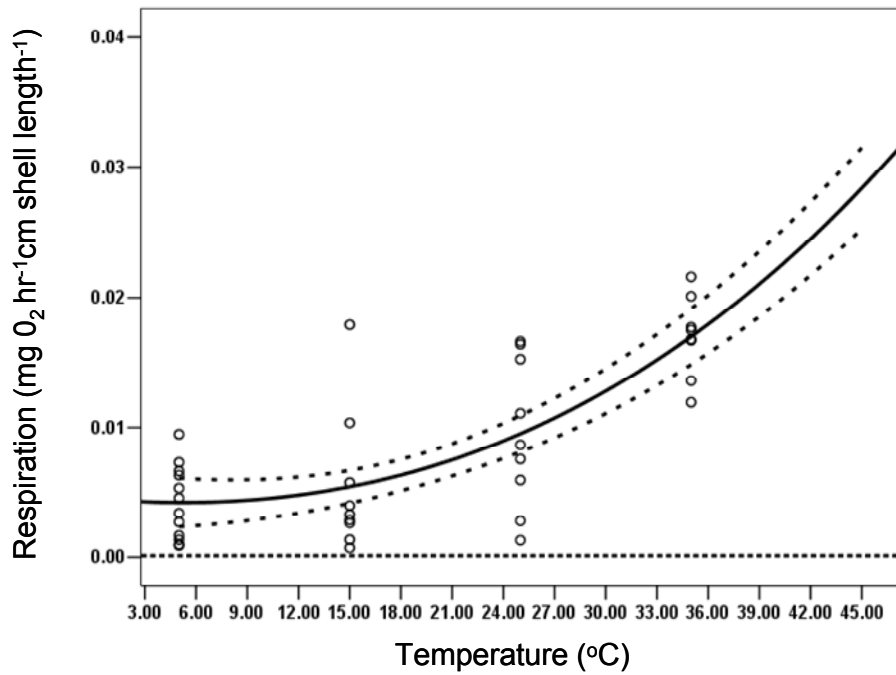
18

Figure 9. Physiological response of *A. plicata* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.

Figure 10. Physiological response of *Q. pustulosa* to acclimation temperatures. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.
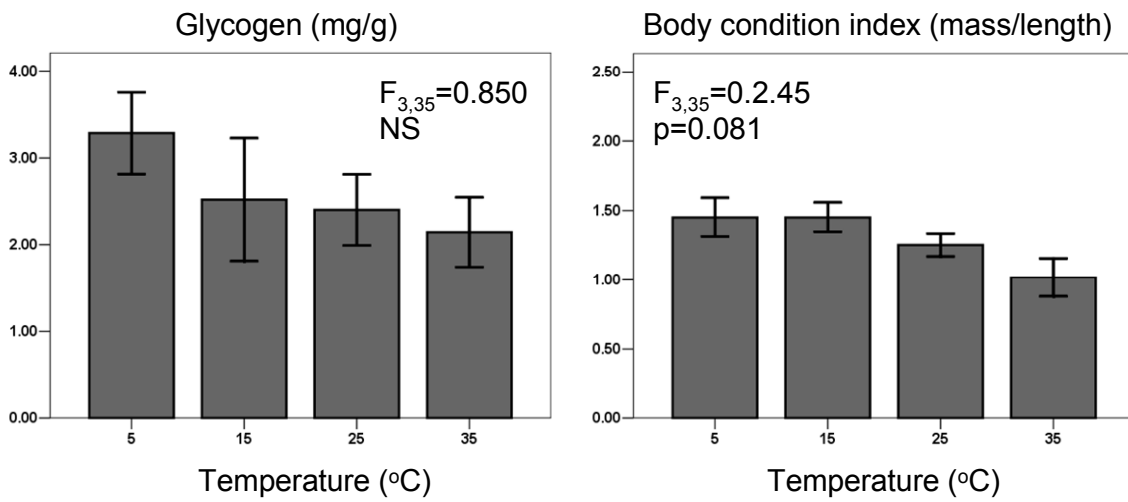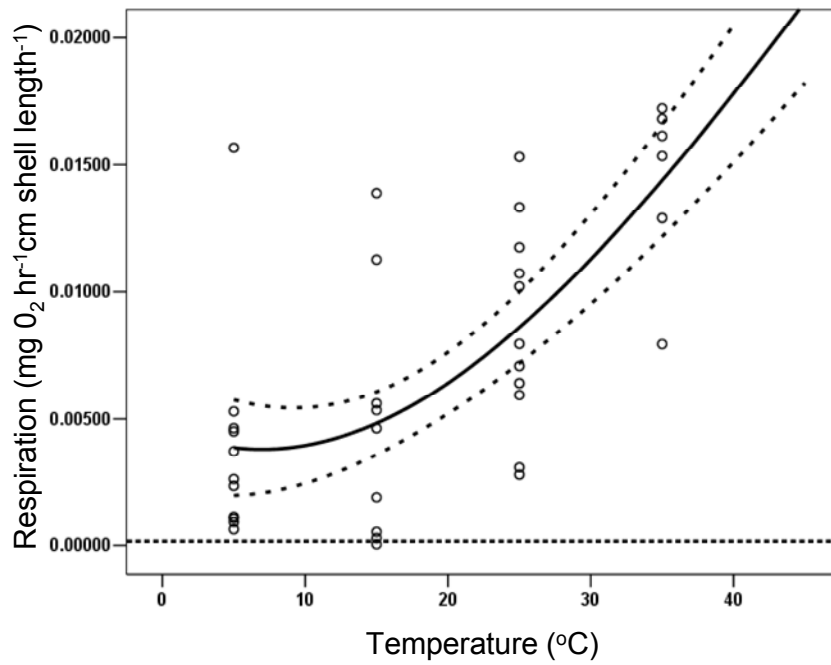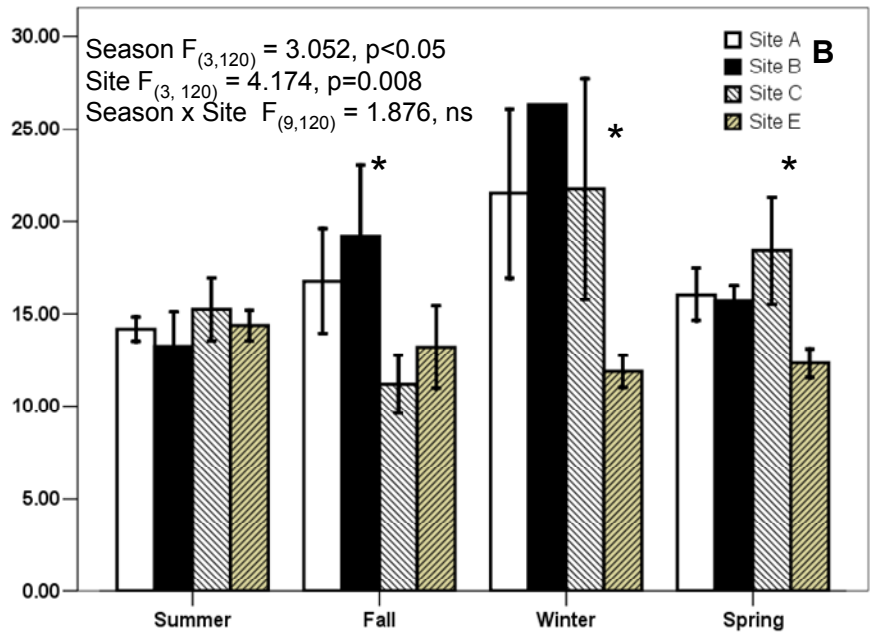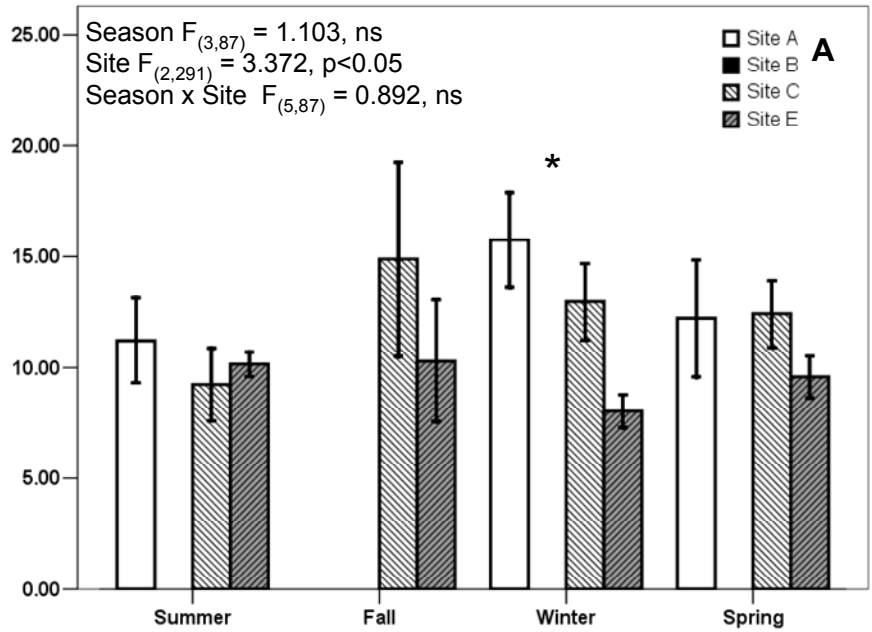
Figure 11. Field derived glycogen concentrations for (A) *A. ligamentina* and (B) *A. plicata.*
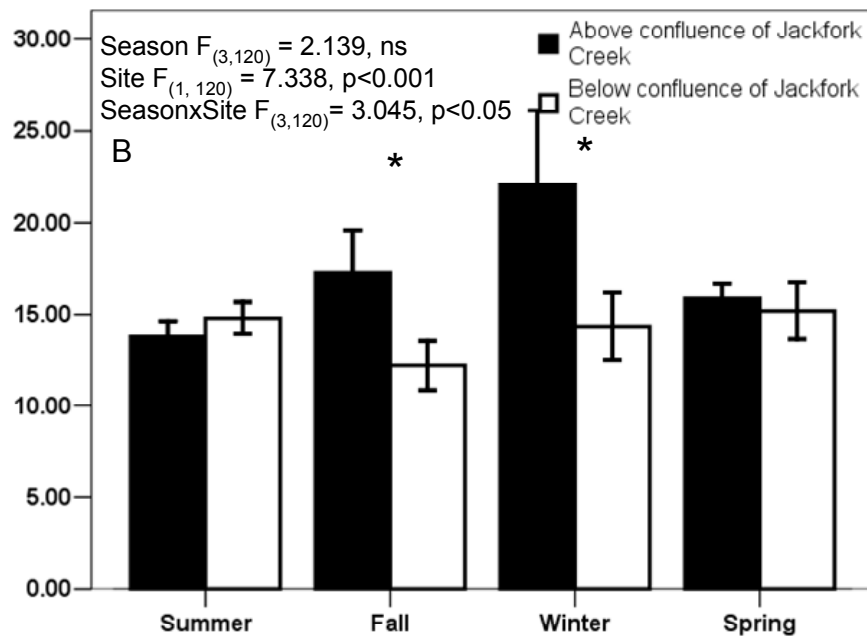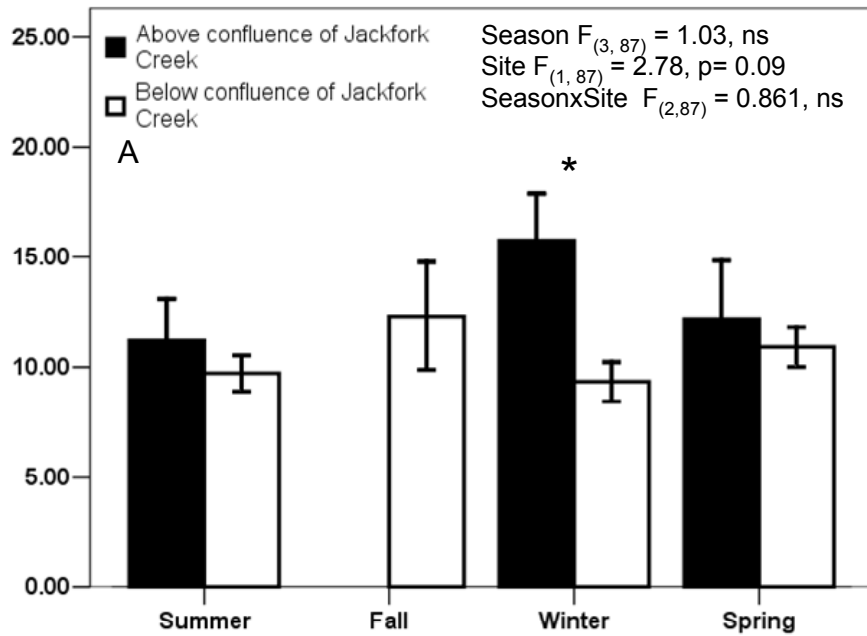
Figure 12. Field derived glycogen concentrations for (A) *A. ligamentina* and (B) *A. plicata.*
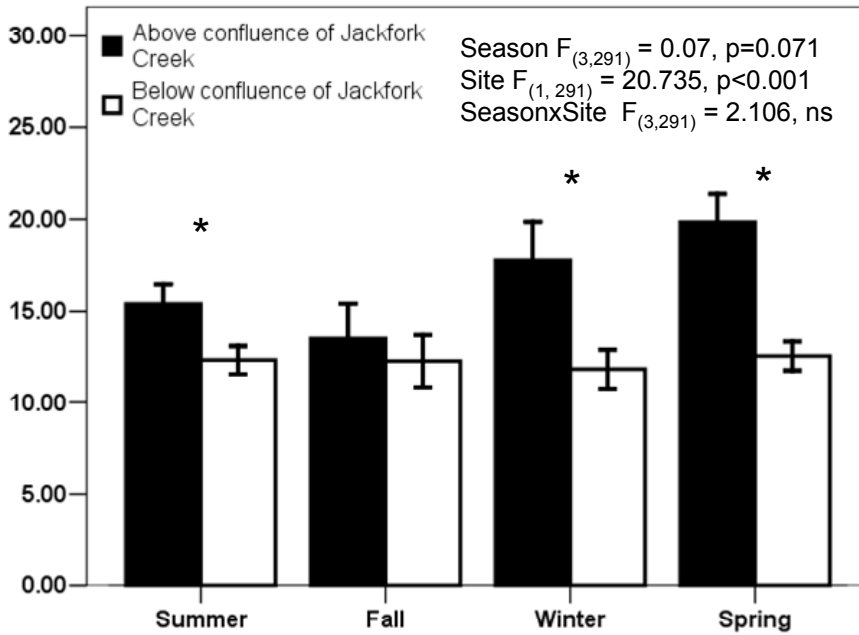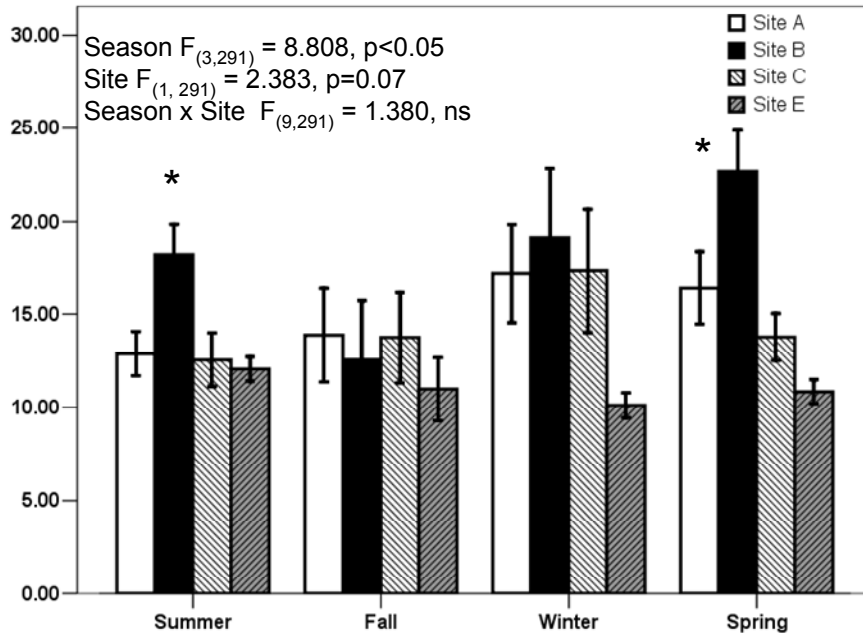
Figure 13. Field derived glycogen concentrations for pooled species.

23
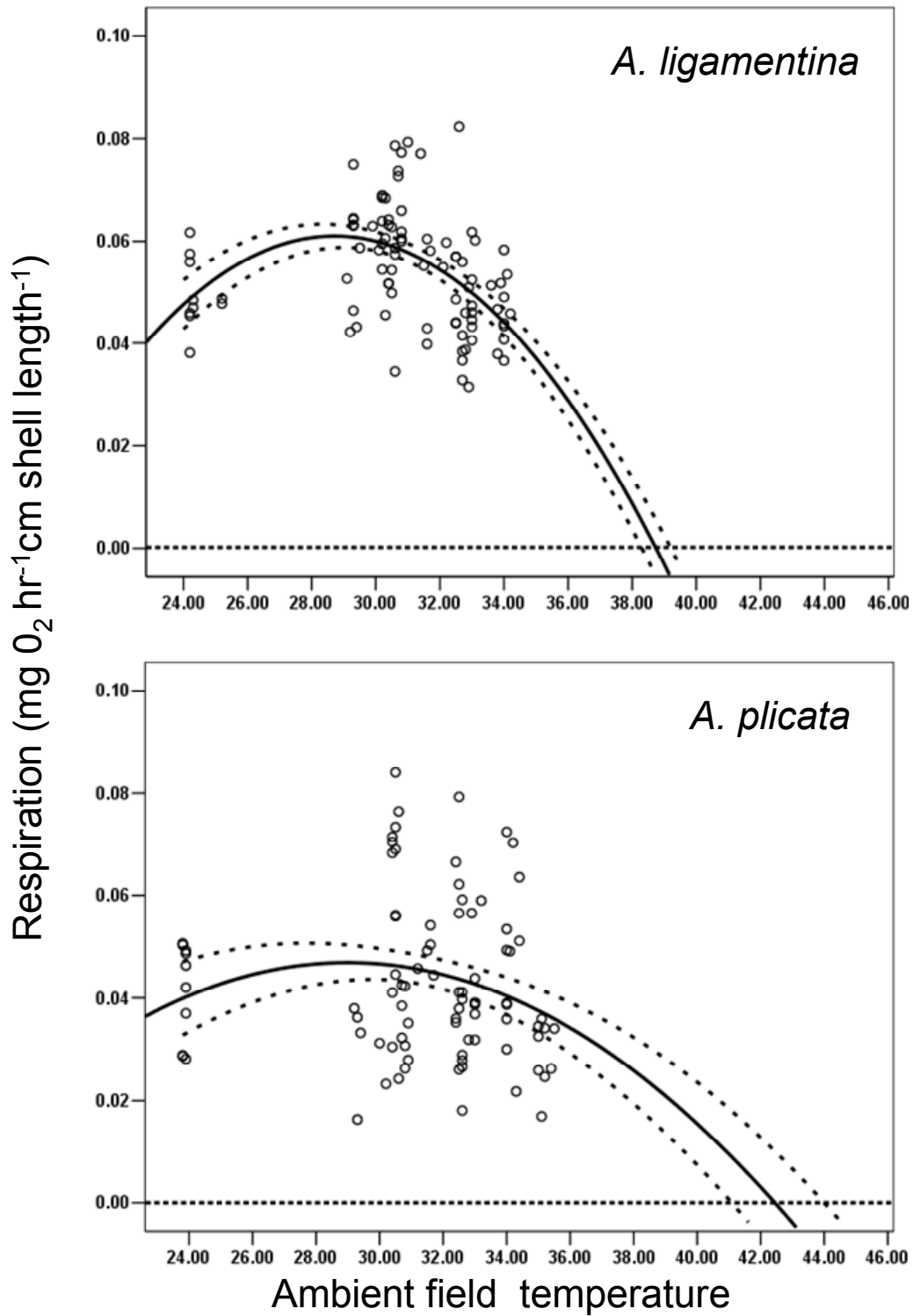
Figure 14. Field derived respiration rate. *A. ligamentina* respiration declines and approaches zero before *A. plicata* suggesting it has a lower thermal threshold. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line).
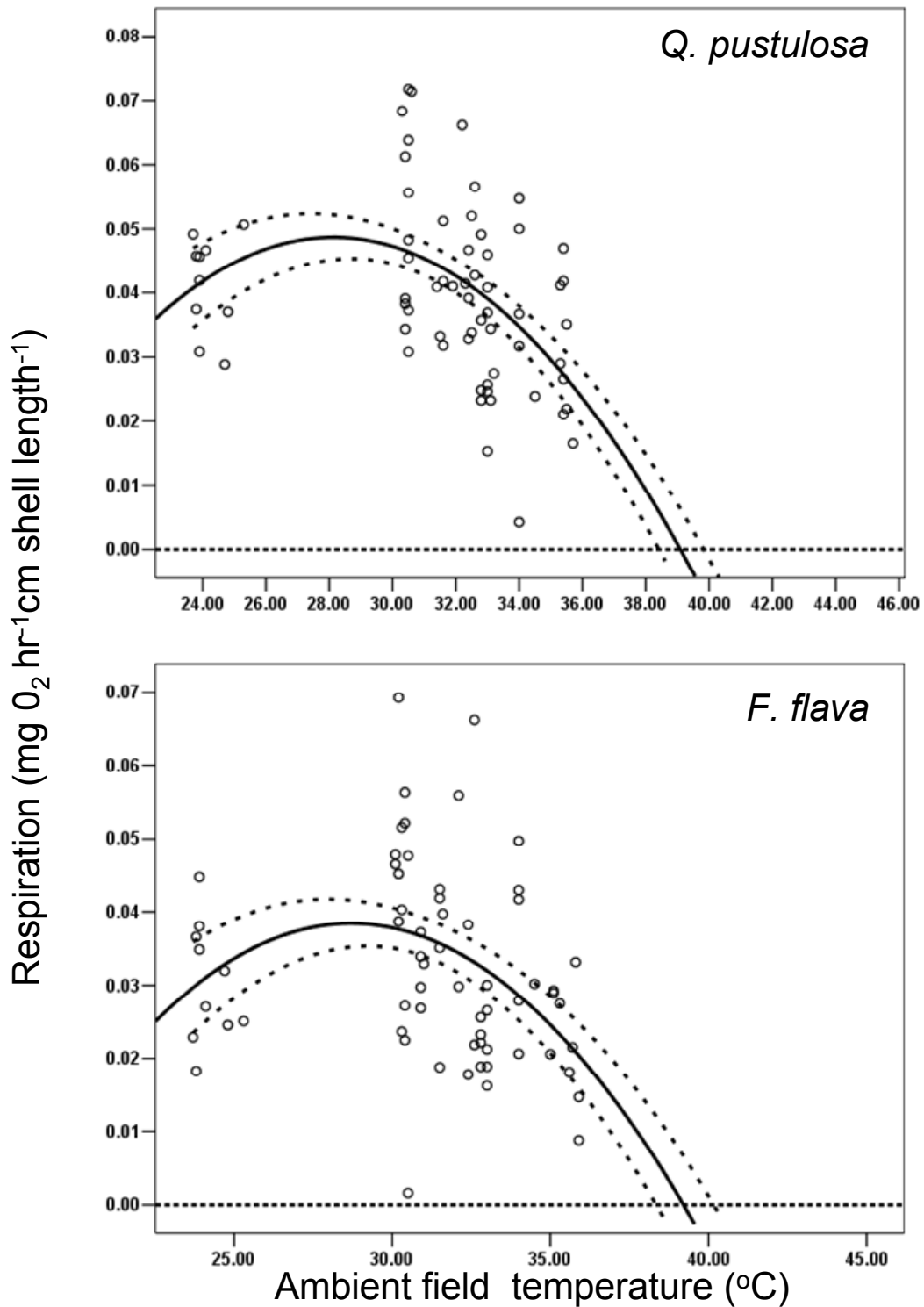
Figure 15. Field derived respiration rate for *Q. pustulosa* and *F. flava*. Dashed lines represent 95% confidence intervals surrounding the regression model (solid line). The y- intercept represents the point at which respiration approaches zero as a result of thermal stress.
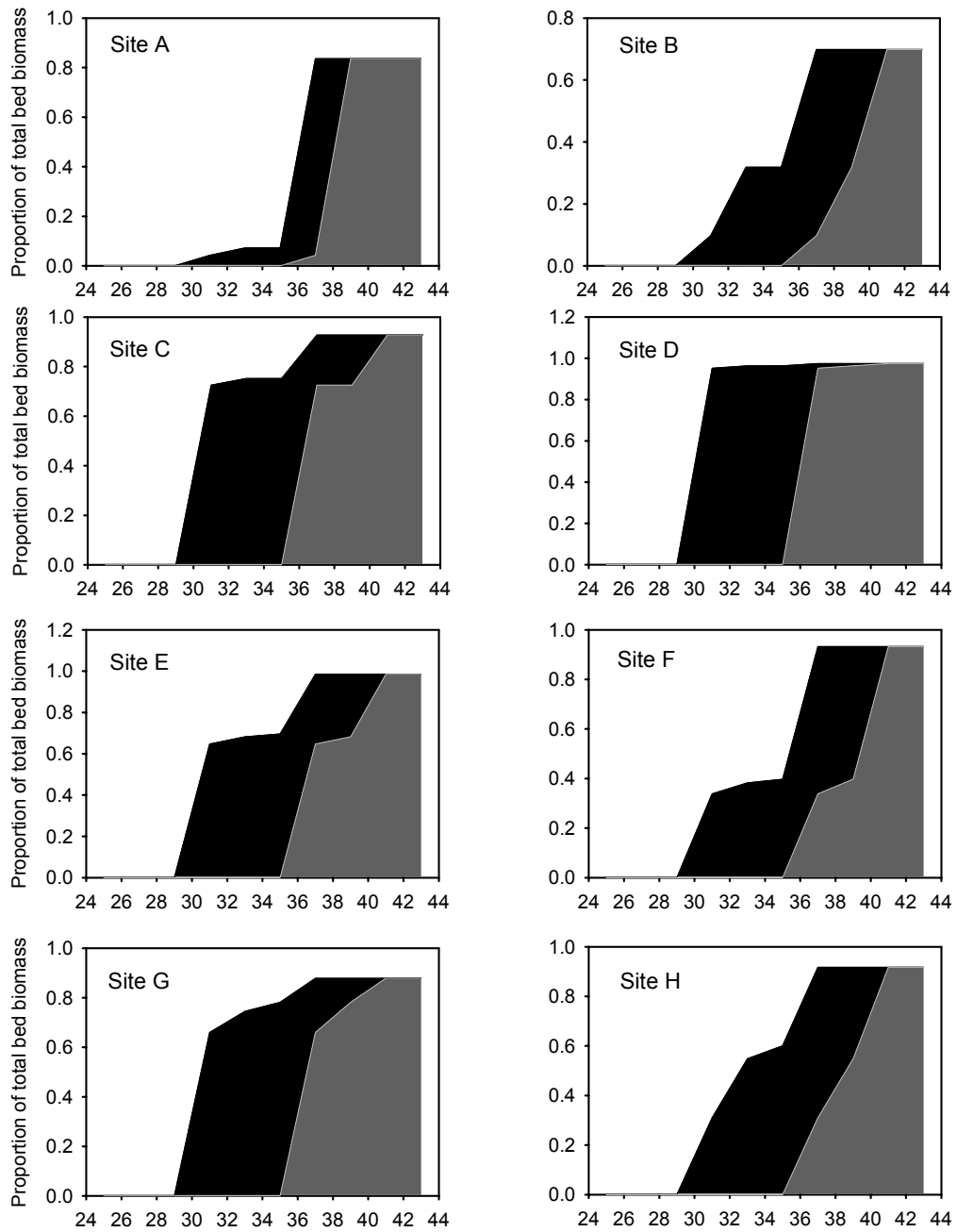
**Figure 16.** Relative proportion of mussels exposed to low stress (dark shade) and high stress (grey shade) water temperatures for each site.
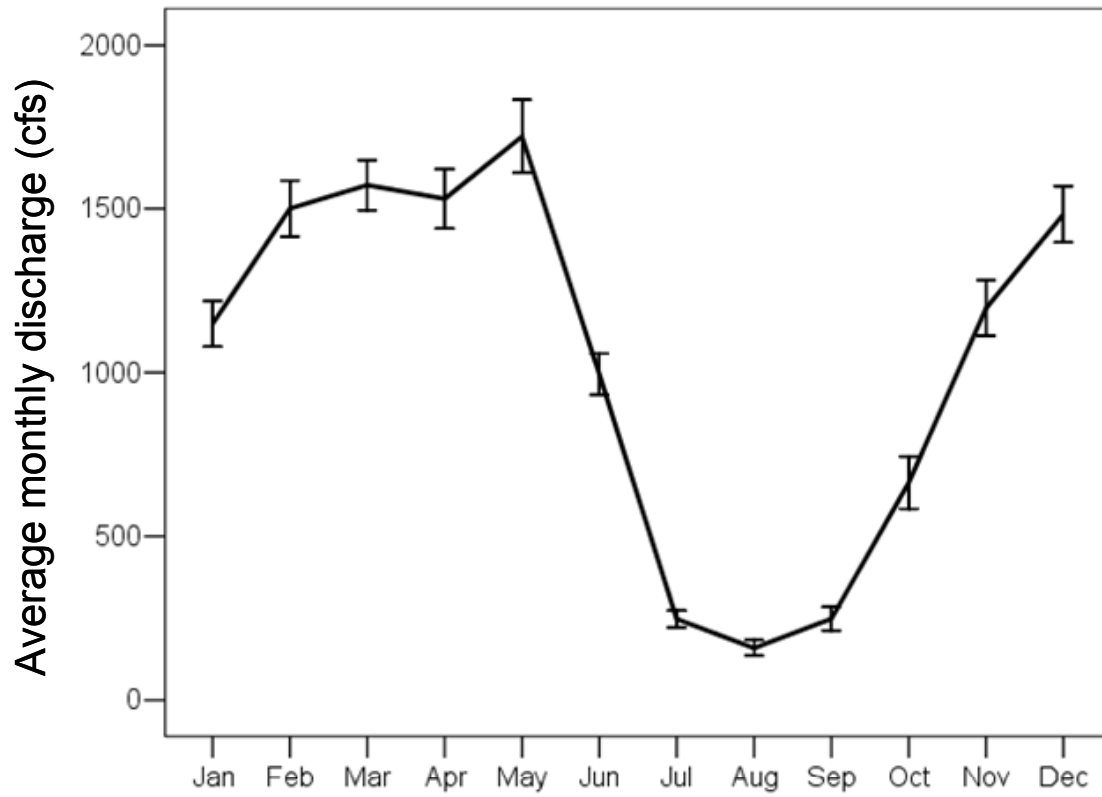
Figure 17. Average monthly stream discharge at Clayton hydrologic monitoring station (1980-1994). Data courtesy of USGS.
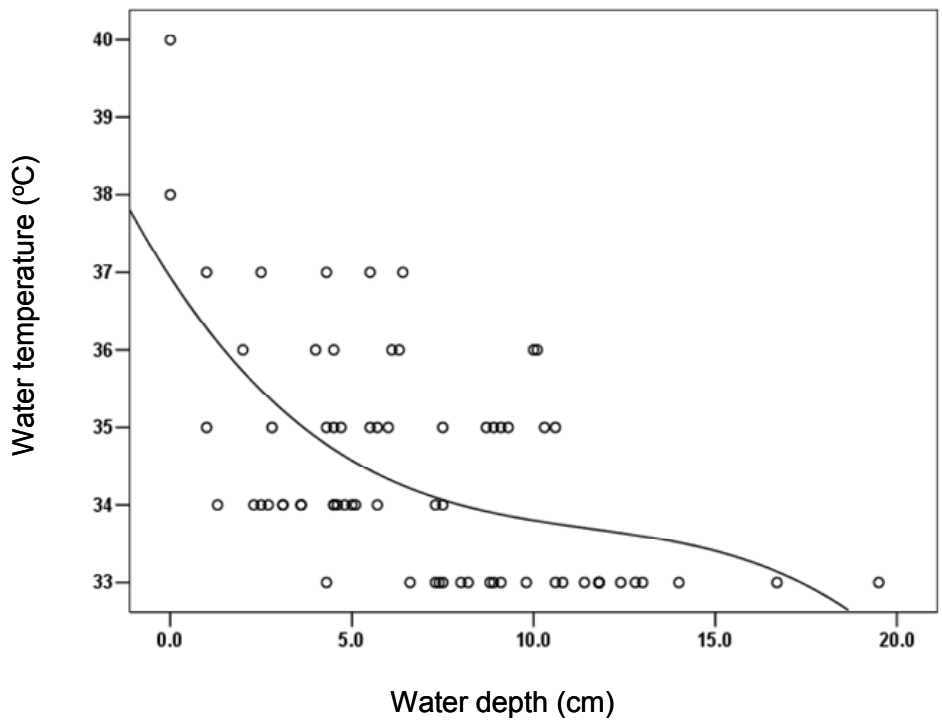
Figure 18. Relationship between depth of water (cm) and ambient water temperature (ºC). Each data point represents local conditions measured within a quadrat.

Locality	GPS co-ordinates (UTM)	
A	15S 311670	3836912
B	15S 0289270	383260
C	15S 0285173	3828341
D	15S 0273144	3824160
E	15S 0262822	3812539
F	15S O262789	3810754
G	15S 0257481	3802920
H	15S 0258288	3793505

Table 1. Locality GPS co-ordinates

Site	model	statistics	parameter
Site A	discharge	$R^2=0.032$, $F_{1,301}=9.84$ $p<0.05$	
	Average air temp Clayton (Tav)	$R^2=0.724$ $F_{2,301}=789.1$ $p<0.001$	
	Discharge, (Tav)	$R^2=0.723$ $F_{1,300}=394.3$ $p<0.001$	
	$Y=b_o+b_1(Tav)+b_2(Tav)^2$	$R^2=0.740$ $F_{2,300}=427.2$ $p<0.001$	$b_0=6.062$ $b_1=0.408$ $b_2=0.013$
Site C ***model can also be used to predict site D.*	discharge	$R^2=0.018$, $F_{1,433}=7.8$ $p<0.05$	
	Average air temp Clayton (Tav)	$R^2=0.781 F_{1,432}=1545.7$ $p<0.001$	
	Discharge, (Tav)	$R^2=0.782 F_{1,432}=776.3$ $p<0.001$	
	$Y=B_o+b_1(Tav)+b_2(Tav)^2$	$R^2=0.788$, $F_{2,432}=800.8$ $p<0.001$	$b_0=5.991$ $b_1=0.576$ $b_2=0.009$
Site E ***model can be used to predict sites F,G, and H.*	discharge	$R^2=0.041$, $F_{1,425}=0.731$ $p>0.05$	
	Average air temp Clayton (Tav)	$R^2=0.690$, $F_{1,657}=1461$ $p>0.001$	
	Discharge, (Tav)	$R^2=0.736$, $F_{1,424}=595.9$ $p>0.001$	
	$Y=B_o+b_1(Tav)+b_2(Tav)^2$	$R^2=0.718$, $F_{2,656}=836.1$ $p>0.001$	$b_0=6.277$ $b_1=0.260$ $b_2=0.019$

Species	Subfamily
Actinonaias ligamentina	Lampsilinae
Amblema plicata	Unioninae
Fusconaia flava	Unioninae
Lampsilis cardium	Lampsilinae
Megalonaias nervosa	Unioninae
Obliquaria reflexa	Lampsilinae
Quadrula pustulosa	Unioninae
Truncilla truncata	Lampsilinae

Table 3. Species used for empirical physiology models.

Species	statistic	model
A. ligamentina	$R^2=0.499$, $F_{3,33}=10.6$ p=0.001	Resp =0.023-0.005(temp)-5.3E^{-6}(temp)^3
A. plicata	$R^2=0.575$, $F_{3,37}= 15.3$ p<0.001	Resp =0.005-1.05E^{-5}(temp)^2+8.6E^{-8}(temp)^3
F. flava	$R^2=0.417$, $F_{3,40}= 8.8$ p<0.001	Resp 0.005- 0.001(temp)+5.69E^{-5}(temp)^2-8.1E^{-7}(temp)^3
Q. pustulosa	$R^2=0.456$, $F_{3,36}= 9.2$ p<0.001	Resp =0.005+1.98E^{-5}(temp)^2-1.3E^{-7}(temp)^3
L. cardium	$R^2=0.358$, $F_{3,30}= 5.015$ p=0.007	Resp =0.016-0.002(temp)-3.5E^{-6}(temp)^3
M. nervosa	$R^2=0.217$, $F_{3,34}= 2.9$ p=0.053	Resp =0.004+2.44E^{-6}(temp)^2-0.009(temp)^3
O. reflexa	$R^2=0.273$, $F_{3,37}= 4.3$ p<0.001	Resp =0.003-2.82E^{-6}(temp)^2-0.011(temp)^3
T. truncata	$R^2=0.469$, $F_{3,37}= 10.0$ p<0.001	Resp =-0.002-2.36^{E-6}(temp)+0.011(temp)^3

Table 4. Empirically derived species-specific models describing the relationship between acclimation temperature and respiration rate.

Species	statistic	model
A. ligamentina	$R^2=0.0.236$, $F_{2,91}=13.73$ $p=0.001$	Resp = 0.035(temp)-0.001(temp)^2-0.438
A. plicata	$R^2=0.041$, $F_{2,86}= 1.778$ $p >0.05$	Resp = 0.015(temp) -0.171
F. flava	$R^2=0.144$, $F_{2,63}= 5.143$ $p<0.001$	Resp = 0.020(temp)-0.248
Q. pustulosa	$R^2=0.203$, $F_{2,65}= 8.0$ $p<0.001$	Resp =0.023(temp)-0.272

Table 5. Field derived species-specific models describing the relationship between acclimation temperature and respiration rate.

***Part II. Review and summarization of literature pertaining to mussels of the Kiamichi
and Little watersheds, Oklahoma.***

B. OBJECTIVES

Summarize the available body of knowledge on general impacts of hydrologic alterations
on unionid mussels and on mussel assemblages of the Kiamichi and Little River systems.

C. NEED

Little River (including its major tributaries the Glover River and the Mountain Fork
River) and the Kiamichi River, are threatened by a water development plan to sell water
to the North Texas Water Alliance. The plan calls for water to be diverted from the
Kiamichi River below Lake Hugo and the Little River near Idabel and below the
Mountain Fork River. Changes in the natural flow regime in these rivers may negatively
impact freshwater mussel populations, including populations of the endangered Ouachita
Rock Pocketbook Mussel, *Arkansia wheeleri*. To determine how changes in the natural
flow regime may impact mussel populations, we must first summarize the existing data
on mussel populations in these rivers and their ecological requirements.

D. APPROACH

We collated all available information historical and current mussel assemblages of the
Little and Kiamichi River watersheds in southeastern Oklahoma, and on impacts of
hydrologic alterations on unionid mussels. Information was obtained from the published
literature and by contacting researches who work in this area.

E. RESULTS AND DISCUSSION

(1) General impacts of hydrologic alterations on unionid mussels

The freshwater mussel (Unionidae) fauna of North America is the most diverse in the
world, but is highly threatened (Bogan 1993), with major declines of mussel populations
and species diversity occurring over the past century (Neves 1992; Neves *et al.* 1997;
Ricciardi *et al.* 1998; Vaughn & Taylor 1999; McMahon & Bogan 2001). Currently, the
U.S. Fish and Wildlife Service recognizes 12% of the native mussel fauna as extinct and
23% as threatened or endangered, and The Nature Conservancy considers 68% of the
U.S. unionid species at risk, compared to only 17% for mammals and 15% for birds
(Biggins & Butler 2000). Recent work has demonstrated that unionid mussels provide
important ecosystem services in the rivers where they are abundant (Kasprzak 1986;
Welker & Walz 1998; Vaughn *et al.* 2004a). Mussels are natural 'biofilters' that remove
algae, bacteria and particulate organic matter from the water column. They influence
nutrient dynamics in freshwaters through excretion as well as biodeposition of feces and
pseudofeces (rejected food particles). By burrowing in the sediment they increase

sediment water and oxygen content, and release nutrients from the sediment to the water column. Finally, the physical presence of both living mussels and their spent shells stabilizes sediment and creates habitat for other benthic organisms (Vaughn & Hakenkamp 2001; Spooner 2002; Strayer *et al.* 2004). Thus, the overall decline of this fauna may have long-term, negative consequences for the functioning of river ecosystems (Strayer *et al.* 1999; Vaughn & Hakenkamp 2001; Vaughn *et al.* 2004a).

Unionid mussels possess a suite of traits that make them highly vulnerable to habitat disturbance (Table 1). Although fecundity is high, the odds of an egg successfully becoming an adult mussel are quite low. Unionids have a complex life history in which the larvae (glochidia) are obligate ectoparasites on the gills and fins of fish. The glochidia of many mussel species can only survive on a narrow range of fish-host species (Kat 1984; Watters 1993; McMahon & Bogan 2001). Once they have metamorphosed from the glochidial stage, juveniles must be deposited in favorable habitat in order to survive. Successful settlement of juveniles appears to be particularly affected by disturbance (Layzer & Madison 1995), and the demography of many mussel populations in disturbed areas is marked by periods when entire year classes are not recruited (Payne & Miller 1989). Because only larvae (attached to fish) can move between mussel beds, and juvenile survival is low (Yeager *et al.* 1994; Sparks & Strayer 1998), potential mussel colonization rates are low (Vaughn 1993). Reproductive maturity of unionid mussels is not reached until at least age 6 and most species live greater than 10 years, with some living as long as 100 years (Imlay 1982; McMahon & Bogan 2001). Once mature, adults in undisturbed habitat exhibit high survivorship (McMahon & Bogan 2001). However, adult mussels are sedentary; movements are seasonal and on a scale of a few to an estimated maximum 100 meters (Green *et al.* 1985; Waller *et al.* 1999). Therefore, unlike many stream organisms such as fish and aquatic insects (Townsend 1989; Matthews 1998), adult mussels have limited refugia from disturbance events in streams. In addition, the filter-feeding habits of mussels make them especially vulnerable to sedimentation and chemical pollution events (Havlik & Marking 1987).

Table 1. Life history traits of unionid mussels. Modified from McMahon & Bogan (2001) and Mehlhop & Vaughn (1994).

Life span	< 6 to > 100 yr
Age at maturity	6 – 12 yr
Strategy	Iteroparous
Fecundity	200,000 – 17,000,000
Reproductive efforts per year	Typically 1
Juvenile size	50 – 400 um
Relative juvenile survivorship	Very low
Relative adult survivorship	High in undisturbed habitats
Larval habitat	Obligate parasite on fish

The majority of mussel species are most successful where water velocities are low enough to allow substrate stability but high enough to prevent excessive siltation (Vannote & Minshall 1982; Hartfield & Ebert 1986; Strayer 1993; Strayer 1999). Because of this dependence on appropriate substrate and flow conditions, mussels are naturally patchily distributed in many rivers, often occurring in densely aggregated multi-species "beds" separated by areas where mussels occur sporadically or not at all (Strayer *et al.* 1994; Strayer *et al.* 2004). These habitat characteristics have been difficult to quantify, and mussels are often absent from areas that visually appear to be good habitat (Strayer 1993; Strayer & Ralley 1993; Vaughn *et al.* 1995; Strayer *et al.* 2004). Conventional methods for estimating instream flow preferences for mussels have been largely unsuccessful (Gore et al. 2001). Layzer & Madison (1995) investigated the use of instream flow incremental methodology (IFIM) for determining microhabitat preferences of mussels in Horse Lick Creek, Kentucky. They found that results were flow conditional; i.e. because mussels are non-mobile and have highly clumped distributions, they appeared to prefer different hydraulic conditions at different stream discharges. However, unlike simple hydraulic variables such a depth and velocity, complex hydraulic characteristics such as shear stress were significantly correlated with mussel abundance (Layzer & Madison 1995). Strayer (1999) found that mussel beds were located in areas protected from high flows and subsequent shear stress and Hardison & Layzer (2001) found that shear velocity varies on a small spatial scale within mussel beds and is negatively correlated with mussel density.

The major cause of mussel decline in the U.S. is from the alteration of the natural flow regime of rivers, primarily by impoundments and channelization (Neves 1992; Allan & Flecker 1993; Bogan 1993; Watters 1996; Neves *et al.* 1997; Master *et al.* 1998; Vaughn & Taylor 1999; Watters 1999). The ways in which impoundments alter existing stream habitat and processes have been extensively described (Baxter 1977; Petts 1984; Yeager 1993; Ligon *et al.* 1995; Sparks 1995). Many mussels do poorly in the altered conditions within impoundments, which include general lack of flow, sedimentation, and frequent anoxic conditions in deeper areas (Haag & Thorp 1991; Watters 1999). Several dozen mussel species have been driven to extinction wholly or in large part by the construction of dams (Layzer *et al.* 1993; Lydeard & Mayden 1995; Watters 1999); nearly without exception impounded rivers have lost or changed their mussel faunas (Blalock & Sickel 1996; Watters 1999). For example, the mussel fauna of the Chickamauga Reservoir portion of the Tennessee River remained essentially unchanged for 2000 years prior to impoundment. After impoundment, over 30 species were extirpated and several are now extinct (Parmalee *et al.* 1982; Watters 1999).

Mussel populations also are impacted up and downstream of impoundments. River sections below impoundments are substantially different than free-flowing rivers (Yeager 1993; Poff *et al.* 1997). Effects include altered seasonality of flow and temperature regimes, changed patterns of sediment scour and deposition (Anderson et al. 1991), and altered transport of particulate organic matter, the food base for mussels (Petts 1984; Frissell *et al.* 1986; Ward & Stanford 1987; Ligon *et al.* 1995). Numerous studies have documented mussel declines below impoundments (Suloway *et al.* 1981; Miller *et al.* 1984; Williams *et al.* 1992a; Layzer *et al.* 1993; Vaughn & Taylor 1999; Garner &

McGregor 2001). For example, the Kaskaskia River supported 40 mussel species prior to impoundment; eight years after impoundment the species count was down to 24 species, some sites no longer supported any mussels, and abundance had declined (Suloway *et al.* 1981; Watters 1999).

Hydrologic alterations impact mussels both directly through physical stress, such as temperature, siltation, and scour, and indirectly through changes in habitat, food, and fish-host availability. Fluctuating discharge alters the transport of the particulate material in the water column that is the primary food source for mussels. Depending on season and normal seston loads, this can impact mussels. Releases from impoundments often result in both abnormally high and low flows, sometimes on a daily basis, and these often occur at the "wrong" time of year (Yeager 1993; Poff *et al.* 1997; Richter & Richter 2000). Discharge that is either high during the wrong season or high too frequently can have devastating impacts on mussels. High discharge can displace settling juveniles before they have burrowed into the streambed or attached their byssal threads to sediment (Neves & Widlak 1987; Holland-Bartels 1990; Layzer & Madison 1995; Hardison & Layzer 2001). Increased discharge alters the distribution of sediment through scour, flushing, and deposition of newly eroded material from the banks. Mussels are often killed by sediment scour directly below dams (Layzer et al. 1993) and scour is a major reason for the failure of mussel re-introductions (Layzer & Gordon 1993). Sediment deposition clogs mussel siphons and gills (i.e. smothers them) and interferes with feeding and reproduction (Young & Williams 1983; Dennis 1984; Aldridge *et al.* 1987). Erosion caused by increased discharge at one location in a stream results in deposition of the eroded material further downstream, increasing the width-depth ratio of that portion of the channel and the potential for further bedload transport (Frissell et al. 1986). Therefore, increased discharge can cause habitat loss through both sediment deposition and increased bed mobility. Over time, higher base discharge levels and reduced periods between peak flood events decrease habitat complexity by preventing the formation of areas of stabilized sediments (Frissell et al. 1986). As stated above, sediment stability is a critical habitat requirement for most mussels (Di Maio & Corkum 1995; Strayer 1999; Hardison & Layzer 2001).

Discharge that is either low during the wrong season or abnormally low for extended periods of time also negatively impacts mussels. Extended periods of low flow below impoundments results in the stranding of mussels (Fisher & Lavoy 1972; Spooner & Vaughn 2000); mortality in such cases is usually a result of desiccation and/or thermal stress as the temperature buffering capacity of the water is decreased with reduced water volumes (Watters 1999; Spooner & Vaughn 2000). Numerous mussel dieoffs related to the dewatering of tailwaters below dams and subsequent high water temperatures in the remaining shallow water have been documented (Riggs & Webb 1956; Watters 1999) If stranding does not result in mortality, the associated physiological stress reduces mussel condition and ultimately reproductive potential (McMahon & Bogan 2001).   Long periods of excessively reduced discharge often result in the fragmentation of rivers into shallow pools isolated by long reaches of dry riverbed. Within these shallow pools mussel can be exposed to water temperatures exceeding 40ºC. In dry stretches stranded mussels are exposed to air and to solar insolation. Given that mussels are thermo-

conformers without the ability to regulate body temperature, these conditions often result in high mortality rates (Spooner & Vaughn 2000). Mussels in shallow, isolated pools are also exposed to hypoxia from algal production. Unionids are typically tolerant of moderate bouts of hypoxia (as low as 2 mg/l) (Chen 2002); however, other bivalves, such as invasive *Corbicula* have reduced anaerobic capacity resulting in massive die-offs (White & White 1977; Milton & Matthews 1999; Cherry et al. 2005). Ammonia pulses from decaying bivalves kill juvenile unionids and potentially reduce the condition of adult mussels (Cherry et al. 2005; Cooper et al. 2005).

Water temperature is especially critical to mussels and they deal with thermal stress in a variety of ways. In the event of dewatering, some species can move either vertically into the sediment or horizontally to deeper areas; this strategy can be energetically costly depending on substrate texture and the distance to cooler water (McMahon & Bogan 2001). A second strategy to contend with emersion is direct transfer of oxygen across the mantle edge exposed to the air, which mussels control by gaping. This approach is limited to environments with high humidity and moderate temperature (Dietz 1974). A third strategy is to close the valves and anaerobically catabalyze stored energy reserves. The success of this strategy depends on the amount of energy reserves available and the duration of dewatering (McMahon & Bogan 2001). The main anaerobic storage pathway for mussels is glycogen catabolism. Glycogen is easily transferred to glucose through glucogenesis and its metabolites are non-toxic (Chen 2003) (unlike catabolism of protein which produces toxic ammonia by products); however, shifts in hemolymph pH due to metabolites produced by glycogen catabolism must be buffered by the sequestration of carbonated from the shell (Byrne et al. 1991; McMahon 2000). Given that anaerobic catabolism is an underlying mechanism for emersion survival, factors that control glycogen storage capacity should directly influence the ability of mussels to survive drought events.

Reductions in water temperature below hypolimnetic release dams have been shown to reduce and even eliminate mussel populations for long distances (Ahlstedt 1983; Miller *et al.* 1984; Yeager 1993; Lydeard & Mayden 1995; Vaughn & Taylor 1999). Release of cold water during the summer when water temperatures should be warm suppresses mussel metabolic rates during a time of year when growth should be high (McMahon & Bogan 2001) and inhibits reproduction (Layzer et al. 1993). Coldwater releases also may eliminate or inhibit reproduction of some species of warmwater fishes (Layzer *et al.* 1993; Yeager 1993) and increase the success of introduced coldwater species such as trout. Therefore, abnormally cold discharge, particularly in summer, may act as a permanent colonization barrier to mussels (Vaughn & Taylor 1999).

Because mussels are dependent on fish hosts, any effects of hydrologic alterations on fish hosts also impacts mussel populations. Distribution, abundance, and movement patterns of fish hosts have been shown to be critical to the distribution and abundance of mussels (Watters 1993; Vaughn 1997; Haag & Warren 1998; Vaughn & Taylor 2000). The disappearance of mussel species from several rivers has been linked to the disappearance of the appropriate fish host (Kat & Davis 1984), and mussels have re-colonized rivers after their fish hosts were re-introduced (Smith 1985). Lowhead dams have been shown

to block fish-host migration and lead to the extirpation of mussels in reaches above the dams (Watters 1996). Altered flow regimes can decrease both the species richness and abundance of fish communities (Gore & Bryant 1986; Kinsolving & Bain 1993; Scheidegger & Bain 1995), potentially eliminating mussel hosts. Impacts likely vary both seasonally and with river microhabitat. For example, a high proportion of nest-building fish species, such a centrarchids, are common mussel hosts (Kat 1984; Watters 1994). Thus, altered hydrology that impacts or prevents nesting could result in mussel glochidia failing to attach to hosts, and reduced mussel recruitment.

Mussels evolved in rivers that typically experienced seasonal periods of low and high flow. Recent studies indicate that instream flow needs are not the same for all mussel species (Hardison & Layzer 2001) and that natural, temporal variability in flows is important to maintaining diverse mussel assemblages. For example, recruitment of some species seems to be greatest at below average discharges, while other species require a more normal flow rate for successful recruitment (Gore et al. 2001). To maintain diverse mussel communities, annual hydrographs may need to vary seasonally and annually to provide optimal flows for different groups of species (Gore et al. 2001).

(2) Mussels of southeastern Oklahoma Rivers

(2a) Historical information

Based on archeological evidence, the overall mussel species composition of southeastern Oklahoma rivers has changed little over the last several thousand years. For example, all mussel species identified from a Caddo Indian midden (ca. 3500-1000 B.P.) near the Poteau River, were found in the Poteau River in the last decade (Bell 1953; Wyckoff 1976; White 1977; Vaughn & Spooner 2004). No mussel species are known to be entirely extirpated from either the Kiamichi (Vaughn et al. 1996) or Little Rivers (Vaughn & Taylor 1999), the two rivers in the region that have been studied the most extensively.

While few rivers in the region have lost species outright, within rivers both the number of sites at which species occur and species abundances have declined. The recent fauna was first surveyed by Isely in the early 1900s (Isely 1911, 1914; Isely 1924; Isely 1931). He conducted a comprehensive distributional survey of the mussel fauna of the Red River drainage, focusing on the eastern half of Oklahoma, as part of a nation-wide effort by the U.S. Bureau of Fisheries to find mussel populations to harvest for the pearl-button industry. Isely sampled 20 sites in the Red River drainage from 1910-1912 (Isely 1924); six of these sites are now under impoundments. In the 1960s Valentine and Stansbery (1971) collected from 9 sites, including one that had previously been sampled by Isely; one of these sites has been inundated by an impoundment. From 1990-1995 Vaughn (2000) re-sampled 19 sites in the Red River drainage, the majority in southeastern Oklahoma, that had been sampled historically by Isely and Valentine and Stansbery. She found that species richness decreased at 89% of the sites and that 86% of species occurred at fewer sites than in the past. Vaughn used these data to calculate local extinction rates (extinction rate from a local patch or site, not the river as a whole). Local

extinction rates were significantly greater than colonization rates, indicating that mortality of mussels is exceeding recruitment in the region (Vaughn 2000).

In the early 1990s Vaughn & Taylor (1999) examined the distribution and abundance of mussels along a 240 km length of the Little River in Oklahoma, from above Pine Creek reservoir to the state line. They observed a mussel extinction gradient downstream from impoundments in the watershed. With increasing distance from Pine Creek Reservoir, an impoundment of the mainstem Little River, there was a gradual, linear increase in mussel species richness and abundance. Rare species only occurred at sites furthest from the reservoir. These same trends were apparent below the inflow from the Mountain Fork River, which is impounded upstream as Lake Broken Bow, and mussel abundance was greatly reduced. In both situations, below reservoir inflows abundance of even common, widespread mussel species was greatly reduced. Thus, even though no species extirpations are known from the Little River, the biological integrity of numerous subpopulations has been greatly decreased by the loss of individuals (Vaughn & Taylor 1999).

The lower Kiamichi River is impounded by Hugo Reservoir. Jackfork Creek, a tributary of the Kiamichi, flows into the river approximately half way down its 180 km length. Jackfork Creek is impounded by Sardis Reservoir. This creek is the largest tributary of the Kiamichi, contributing nearly 30% of the average river flows at the confluence of the two streams. During recent drought years, water that would normally drain into the Kiamichi has been held in Sardis Reservoir, exacerbating drought conditions and causing sections of the Kiamichi to stop flowing and in some cases go completely dry. The summer of 2000 was particularly harsh because of higher than average air temperatures and no rain. During the summer of 2000 Spooner and Vaughn (2000) monitored the effect of these extremely low water levels on a mussel assemblage in the lower Kiamichi near Moyers for which we had two previous years of population data; at this particular site, there was no flow and water temperature during our sampling exceeded 40°C. Mussel mortality was significantly correlated with water depth, with the highest survival in the deepest, coolest water. Mortality was species-specific, with smaller mussels appearing to be hardest hit. Mortalities of federally endangered species were observed (*A. wheeleri* (1 individual) and *L. leptodon* (1 individual)); both individuals were found freshly dead, with tissue still attached, suggesting that the recent mortality was due to the drought and high water temperature. In an effort to minimize mortality, The Army Corps of Engineering released a series of 12 cfs (cubic feet per second) surges of water from Sardis Reservoir resulting in a 4.4 cfs spike in discharge at Clayton and a 1.2 cfs spike at Antlers. Unfortunately, because to the riverbed was already very dry, most of the flow was lost to the water table, and the release was insufficient to reduce water temperature for mussels.

(2b) Current mussel fauna

Despite the declines discussed above, the four rivers of far southeastern Oklahoma (Kiamichi, Little, Glover and Mountain Fork) continue to harbor a rich and overall healthy mussel fauna. There are approximately 52 extant unionid mussel species known

to presently occur in Oklahoma waters (Williams et al. 1992b; Oklahoma Natural Heritage Inventory database), and 41 of these (80%) occur in these rivers (Table 2). In 1998, The Nature Conservancy identified the Interior Highlands (which includes the four rivers in question) as one of the most critical regions in the U.S. for protecting freshwater biodiversity, based on its rich fish and mussel fauna. Based on a comprehensive national assessment of available data, The Nature Conservancy determined that all of the at-risk freshwater fish and mussel species in the U.S. could be conserved by protecting and restoring 327 watersheds (15% of total US watersheds) across the country; the Kiamichi and Little River watersheds were included in this highly select group (Master et al. 1998). Three federally endangered species occur in these rivers, the Ouachita rock pocketbook, the winged mapleleaf, and the scaleshell. *Arkansia wheeleri*, the Ouachita rock pocketbook mussel, occurs in only three rivers in the world, the Kiamichi and Little rivers in Oklahoma, and in the Ouachita River in Arkansas (Vaughn *et al.* 1993; Vaughn 1994; Vaughn & Pyron 1995; Vaughn *et al.* 1995; Vaughn *et al.* 2004b). The Kiamichi population is considered the most viable; subpopulations are patchily located over a 128 km stretch of the river from near Whitesboro to directly above Lake Hugo. Within these subpopulations, the species is quite rare. Vaughn & Pyron (1995) found that in the Kiamichi River, *A. wheeleri* occurs only in the largest, most species-rich mussel beds. Even its optimal habitat the species was always rare; mean relative abundance varied from 0.2 to 0.7% and the mean density within large mussel beds was 0.27 individuals / m^2. The youngest individual *A. wheeleri* encountered was approximately 12 years of age, indicating that recruitment is low (Vaughn & Pyron 1995).   One of the *A. wheeleri* subpopulations in the Kiamichi is located near the proposed water outtake at Moyers (Vaughn *et al.* 2004b). Two subpopulations of *A. wheeleri* have been identified in the Little River; both of these are located on the U.S. Fish and Wildlife Service Little River Wildlife Refuge (Vaughn *et al.* 1995).

Leptodea leptodon, the scaleshell mussel, was historically distributed throughout much of the Interior Basin but has been extirpated from much of its range (Natureserve, 2005). The species is now restricted to 13 streams in the Interior Highlands, including the Kiamichi River, where it is known from the same site near Moyers that contains the *A. wheeleri* subpopulation discussed above (Vaughn *et al.* 2004b).

Quadrula fragosa, the winged mapleleaf, historically occurred in the Interior Basin from Minnesota to Alabama. Currently, the best population is in the St. Croix River in Wisconsin. A viable population is thought to exist in the Ouachita River in Arkansas (Hove *et al.* 2003). Specimens believed to be *Q. fragosa* have been observed in the Kiamichi River in the past and some individuals believed to be *Q. fragosa* were observed in the Little River in 2005. Tissue was collected from some individuals and sent to an expert for genetic confirmation of species identification. Genetic studies need to be conducted to determine if these are indeed *Q. fragosa*.

Several of the mussel species occurring in the four rivers are endemic to the Ouachita Highlands or Interior Highlands. These include *Arkansia wheeleri*, discussed above, *Ptychobranchus occidentalis* and *Villosa arkansasensis*. *Ptychobranchus occidentalis*, the Ouachita kidneyshell, occurs sporadically throughout the Kiamichi and Little rivers

(Vaughn *et al.* 1996; Vaughn & Taylor 1999), and is a dominant species in the Mountain Fork (Vaughn & Spooner 2000) and Glover rivers (Vaughn 2003b). *Villosa arkansasensis*, the Ouachita creekshell, occurs in the Little, Glover and Mountain Fork rivers (Vaughn & Taylor 1999; Vaughn & Spooner 2000; Vaughn 2003b).

Quadrula cylindrica, the rabbitsfoot mussel, is being considered for listing as an endangered species by the U.S. Fish and Wildlife Service (USFWS 2005). The range of this species has declined significantly. One of the most viable remaining populations is in the Little River in Oklahoma (USFWS 2005) where at least 5 subpopulations exist from just above Idabel through upper portions of Little River Wildlife Refuge (Vaughn et al., unpublished data). A small population occurs in the Glover River above the Highway 3 crossing (Vaughn 2003b).

Table 2. Mussel species that currently occur in the Kiamichi, Little, Glover and Mountain Fork rivers along with their global and state conservation rank and state and federal protection status. These species represent 80% of the known Oklahoma mussel fauna. Data are from (Vaughn & Pyron 1995; Vaughn *et al.* 1996; Vaughn 1997; Vaughn *et al.* 1997; Vaughn & Taylor 1999; Vaughn 2000; Vaughn & Taylor 2000; Vaughn 2003a; Vaughn 2003b; Vaughn *et al.* 2004a; Vaughn & Spooner 2004; Vaughn *et al.* 2004b)

Species	Common name	Kiamichi River	Little River	Glover River	Mt. Fork River	Global Rank	State Rank	Fed Status	State Status
Actinonaias ligamentina	mucket	X	X	X	X	G5	S3		
Amblema plicata	threeridge	X	X	X	X	G5	S3		
Arkansia wheeleri	Ouachita rock pocketbook	X	X			G1	S1	E	E
Ellipsaria lineolata	butterfly	X	X	X		G4	S2		
Elliptio dilatata	spike		X			G5	S1		
Fusconaia flava	Wabash pigtoe	X	X	X	X	G5	S4		
Lampsilis cardium	plain pocketbook	X	X	X	X	G5	S4		
Lampsilis hydiana	Louisiana fatmucket				X	G3G4	S1		
Lampsilis satura	sandbank pocketbook		X			G3	S?		
Lampsilis siliquoidea	fatmucket	X	X	X	X	G5	S?		
Lampsilis teres	yellow sandshell	X	X		X	G5	S5		
Lasmigona complanata	white heelsplitter	X	X			G5	S5		
Lasmigona costata	flutedshell	X	X	X	X	G5	S1		
Leptodea fragilis	fragile papershell	X	X	X		G5	S4		
Leptodea leptodon	scaleshell	X				G1	S1	E	SS2
Ligumia subrostrata	pondmussel	X	X		X	G4	S4		
Megalonaias nervosa	washboard	X	X			G5	S2		
Obliquaria reflexa	threehorn wartyback	X	X			G5	S3		
Obovaria jacksoniana	southern hickorynut	X			X	G1G2	S2		
Plectomerus dombeyanus	bankclimber		X	X		G4	S2		
Pleurobema sintoxia	round pigtoe		X			G4	S2		
Pleurobema rubrum	pyramid pigtoe	X	X			G3	S2		

Species	Common name					G	S	Fed	State
Potamilus purpuratus	bleufer	X	X	X		G5	S4		
Ptychobranchus occidentalis	Ouachita kidneyshell	X	X	X	X	G3G4	S2		
Pyganodon grandis	giant floater	X	X			G5	S5		
Quadrula apiculata	southern mapleleaf		X			G5	S4		
Quadrula fragosa	winged mapleleaf	X				G1	S1	E	
Quadrula cylindrica	rabbitsfoot		X	X		G3	S1		SS2
Quadrula nodulata	wartyback		X			G4	S1		
Quadrula pustulosa	pimpleback	X	X	X	X	G5	S4		
Quadrula quadrula	mapleleaf	X	X	X	X	G5	S5		
Strophitus undulatus	creeper	X	X	X	X	G5	S3		
Toxolasma parvus	lilliput	X	X	X	X	G4	S4		
Toxolasma texasensis	Texas lilliput		X		X	G4	S1		
Tritogonia verrucosa	pistolgrip	X	X	X	X	G4	S4		
Truncilla truncata	deertoe	X	X	X		G4	S4		
Truncilla donaciformis	fawnsfoot		X		X	G4	S4		
Uniomerus tetralasmus	pondhorn			X		G4	S4		
Utterbackia imbecillis	paper pondshell		X			G5	S5		
Villosa arkansasensis	Ouachita creekshell		X	X	X	G2	S1S2		
Villosa iris	rainbow		X	X	X	G5	S1		
Villosa lienosa	little spectaclecase		X	X	X	G5	S2		

F. SIGNIFICANT DEVIATIONS

There were not significant deviations from the original project description.

G. COSTS

H. PREPARED BY

Daniel E. Spooner

Dr. Caryn C. Vaughn

Heather S. Galbraith

I. DATE: December 19 , 2005

J. APPROVED BY

Oklahoma Department of Wildlife Conservation

K. LITERATURE CITED

Allan J.D. & Flecker A.S. (1993) Biodiversity conservation in running waters. *BioScience*, 43, 32-43

Allan J.D., Erickson D.L. & Fay J. (1997) The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology*, 37, 149-161

Ahlstedt S.A. (1983) The molluscan fauna of the Elk River in Tennessee and Alabama. *American Malacological Bulletin*, 1, 43-50

Aldridge D.W., Payne B.S. & Miller A.C. (1987) The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. *Environmental Pollution (Series B)*, 45, 17-28

Anderson R.M., Layzer J.B. & Gordon M.E. (1991) Recent catastrophic decline of mussels (Bivalvia: Unionidae) in the Little South Fork Cumberland River, Kentucky. *Brimleyana*, 17, 1-8

Baker S.M. & Hornbach D.J. (2001) Seasonal metabolism and biochemical composition of two unionid mussels, *Actinonaias ligamentina* and *Amblema plicata*. *Journal of Molluscan Studies*, 67, 407-416

Bauer G. (1998) Allocation policy of female freshwater pearl mussels. *Oecologia*, 117, 90-94

Baxter R.M. (1977) Environmental Effects of Dams and Impoundments. *Ann. Rev. Ecol.*, Syst.8, 255-283

Bell R.E. (1953) The Scott Site, Leflore County, Oklahoma. *American Antiquity*, 18, 314-331

Berg D.J., Haag W.R., Guttman S.I. & Sickel J.B. (1995) Mantle biopsy: a technique for nondestructive tissue-sampling of freshwater mussels. *Journal of the North American Benthological Society*, 14, 577-581

Biggins R.G. & Butler R.S. (2000) Bringing mussels back in the southeast. *Endangered Species Technical Bulletin*

Blalock H. & Sickel J.B. (1996) Changes in the mussel (Bivalvia: Unionidae) fauna within the Kentucky portion of Lake Barkley since impoundment of the lower Cumberland River. *American Malacological Bulletin*, 13, 111-116

Bogan A.E. (1993) Freshwater bivalve extinctions (Mollusca: Unionoida): A search for causes. *American Zoologist*, 33, 599-609

Byrne M. (1998) Reproduction of river and lake populations *Hyridella depressa* (Unionacea: Hyriidae) in New South Wales: implications for their conservation. *Hydrobiologia*, 389, 29-43

Byrne, R.A., Shipman B.N., Smatresk, N.J., Dietz, T.H. & McMahon R.F. (1991) Acid-base balance during emergence in the freshwater bivalve *Corbicula fluminea*. *Physiological Zoology*. 64, 748-766

Chen L.Y. (1998) The respiratory physiology and energy metabolism of freshwater mussels and their responses to lack of oxygen. PhD dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Chen L.Y., Heath A.G. & Neves R.J. (2001) Comparison of oxygen consumption in freshwater mussels (Unionidae) from different habitats during declining dissolved oxygen concentration. *Hydrobiologia*, 450, 209-214

Cope W.G., Newton T.J. & Gatenby C.M. (2003) Review of techniques to prevent introduction of zebra mussels (*Dreissena polymorpha*) during native mussel (Unionoidea) conservation activities. *Journal of Shellfish Research*, 22, 177-184

Cote I.M. & Jelnikar E. (1999) Predator-induced clumping behaviour in mussels (Mytilus edulis Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 235, 201-211

Dennis S.D. (1984) Distributional analysis of the freshwater fauna of the Tennessee River system, with special reference to the possible limiting effects of siltation. In, p. 171. Virginia Polytechnic Institute and State University

Dietz T.H. (1974) Body fluid composition and aerial oxygen consumption in the freshwater mussel, *Ligumia subrostrata* (Say): effects of dehydration and anoxic stress. *Biological Bulletin* 147, 560-572

Di Maio J. & Corkum L.D. (1995) Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. *Canadian Journal of Zoology*, 73, 663-671

Fisher S.G. & Lavoy A. (1972) Difference in littoral fauna due to the fluctuation water levels below a hydroelectric dam. *Journal of the Fisheries Research Board of Canada*, 29, 1472-1476

Frissell C.A., Liss W.J., Warren C.J. & Hurley M.D. (1986) A hierarchial framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, 10, 199-214

Garner J.T. & McGregor S.W. (2001) Current status of freshwater mussels (Unionidae, Margaritiferidae) in the Muscle Shoals area of Tennessee River in Alabama (Muscle Shoals revisited again). *American Malacological Bulletin*, 16, 155-170

Golladay S.W., Gagnon P., Kearns M., M. B.J. & Hicks D.W. (2004) Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwest Georgia. *Journal of the North American Benthological Society*, 23, 494-506

Gore J.A. & Bryant R.M. (1986) Changes in fish and benthic macroinvertebrate assemblages along the impounded Arkansas River. *Journal of Freshwater Ecology*, 3, 333-345

Gore J.A., Layzer J.B. & Mead J. (2001) Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regulated Rivers: Research & Management*, 17, 527-542

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 K.H. & Thorp J.H. (1991) Cross-channel distribution patterns of zoobenthos in a regulated reach of the Tennessee River. *Regulated Rivers: Research & Management*, 6, 225-233

Haag W.R. & Warren M.L. (1998) Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 297-306

Hardison B.S. & Layzer J.B. (2001) Relations between complex hydraulics and the localized distribution of mussels in three regulated rivers. *Regulated Rivers: Research & Management*, 17, 77-88

Hartfield P.D. & Ebert D. (1986) The mussels of southwest Mississippi streams. *American Malacological Bulletin*, 4, 21-23

Havlik M.E. & Marking L.L. (1987) *Effects of contaminants on naiad mollusks (Unionidae): a review*. United State Department of the Interior, Fish and Wildlife Service, Washington, D.C.

Holland-Bartels L.E. (1990) Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. *Journal of the North American Benthological Society*, 9, 327-335

Hove M., M., Berg D.J., DeMarre J., Dietrich K., Gonzales C., Westberg K. & Hornbach D.J. (2003) Historical range expansion of winged mapleleaf provides possibilities for additional reintroduction sites. *Ellipsaria*, 5, 17-18

Imlay M.J. (1982) Use of shells of freshwater mussels in monitoring heavy metals and environmental stresses: a review. *Malacological Review*, 15, 1-14

Isely F.B. (1911) Preliminary note on the ecology of the early juvenile life of the Unionidae. *Biological Bulletin*, 20, 77-80

Isely F.B. (1914) Experimental study of the growth and migration of fresh-water mussels. In: *Report of the U.S. Commissioner of Fisheries for 1913*, pp. 1-26

Isely F.B. (1924) The freshwater mussel fauna of eastern Oklahoma. *Proceedings of the Oklahoma Academy of Science*, 4, 43-118

Isely F.B. (1931) A fifteen year growth record in freshwater mussels. *Ecology*, 12, 616-618

Kasprzak K. (1986) Role of the Unionidae and Sphaeriidae (Mollusca: Bivalvia) in eutrophic Lake Zbechy and its outflow. *Internatinal Revue der Gesamten Hydrobiologie*, 71, 315-334

Kat P.W. (1984) Parasitism and the Unionacea (Bivalvia). *Biological Reviews*, 59, 189-207

Kat P.W. & Davis G.M. (1984) Molecular genetics of peripheral populations of Nova Scotian Unionidae (Mollusca: Bivalvia). *Biological Journal of the Linnean Society*, 22, 157-185

Kinsolving A.D. & Bain M.B. (1993) Fish assemblage recovery along a riverine disturbance gradient. *Ecological Applications*, 3, 531-544

Layzer J.B. & Gordon M.E. (1993) Reintroduction of mussels into the upper Duck River, Tennessee. In: *Conservation and management of freshwater mussels. Proceedings of a symposium, 12 - 14 October 1992, St. Louis, Missouri.* (eds. Cummings KS, Buchanan AC & Koch LM), pp. 89-92, Rock Island, Illinois.

Layzer J.B., Gordon M.E. & Anderson R.M. (1993) Mussels: The forgotten fauna of regulated rivers. A case study of the Caney Fork River. *Regulated Rivers: Research & Management*, 8, 63-71

Layzer J.B. & Madison L.M. (1995) Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Regulated Rivers: Research & Management*, 10, 329-345

Ligon F.K., Dietrich W.E. & Trash W.J. (1995) Downstream ecological effects of dams. *BioScience*, 45

Lydeard C. & Mayden R.L. (1995) A diverse and endangered aquatic ecosystem of the Southeast United Stated. *Conservation Biology*, 9, 800-805

McMahon R.F. (1979) Response to temperature and hypoxia of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Muller). *Comparative Biochemistry and Physiology*, 63a, 383-388.

McMahon R.F. & Bogan A.E. (2001) Mollusca: Bivalvia. In: *Ecology and Classification of North American Freshwater Invertebrates* (eds. Thorp JH & Covich AP). Academic Press

Master L.M., Flack S.R. & Stein B.A. (1998) *Rivers of life: critical watersheds for protecting freshwater diversity*. The Nature Conservancy, Arlington, VA.

Matthews W.J. (1998) *Patterns in freshwater fish ecology*. Chapman & Hall, New York.

Mehlhop P. & Vaughn C.C. (1994) Threats to and sustainability of ecosystems for freshwater mollusks. In: *Sustainable ecological systems: implementing an ecological approach to land management. General technical report Rm-247 for Rocky Mountain Range and Forest Experimental Station.* (eds. Covington W & Dehand LF), pp. 68-77. USDA Forest Service, Fort Collins, Colorado

Miller A.C., Rhodes L. & Tippit R. (1984) Changes in the naiad fauna of the Cumberland River below Lake Cumberland in Central Kentucky. *Nautilus*, 98, 107-110

Milton M.A. & McMahon R.F. (1999) Effects of temperature and temperature acclimation on survival of zebra mussels (*Dreissena polymorpha)* and Asian clams (*Corbicula fluminea*) under extreme hypoxia. Journal of Molluscan Studies, 65, 317-325.

Naimo T.J., Damschen E.D., Rada R.G. & Monroe E.M. (1998) Nonlethal evaluation of the physiological health of unionid mussels: methods for biopsy and glycogen analysis. *Journal of the North American Benthological Society*, 17, 121-128

Neves R.J. (1992) A state-of-the-unionids address. *Symposium on the Conservation and Management of Freshwater Mussels*, 9 (Abstract)

Neves R.J. & Widlak J.C. (1987) Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. *American Malacological Bulletin*, 5, 1-7

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: *Aquatic Fauna in Peril: The Southeastern perspective.* (eds. Benz GW & Collins DE), pp. 45-86. Southeast Aquatic Research Institute, Decatur, GA

Parmalee P.W., Klippel W.E. & Bogan A.E. (1982) Aboriginal and modern freshwater mussel assemblages (Pelecypoda: Unionidae) from the Chicamauga Reservoir, Tennessee. *Brimleyana*, 8, 75-90

Parmalee P.W. & Bogan A.E. (1998) *The Freshwater Mussels of Tennessee*. University of Tennessee, Knoxville.

Payne B.S. & Miller A.C. (1989) Growth and survival of recent recruits to a population of *Fusconaia ebena* (Bivalvia: Mollusca) in the lower Ohio River. *American Midland Naturalist*, 121, 99-104

Petts G.E. (1984) *Impounded rivers*. John Wiley & Sons, New York.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime. *BioScience*, 47, 769-784

Ricciardi A., Neves R.J. & Rasmussen J.B. (1998) Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology*, 67

Richter B.D. & Richter H.E. (2000) Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. *Conservation Biology*, 14, 1467-1478

Richter B.D., Baumgartner J.V., Wigington R. & Braun D.P. (1997) How much water does a river need? *Freshwater Biology*, 37, 231-249

Riggs C.D. & Webb G.R. (1956) The mussel population of an area of loamy-sand bottom of Lake Texoma. *American Midland Naturalist*, 56, 197-203

Scheidegger K.J. & Bain M.B. (1995) Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia*, 1995, 125-135

Schmidt-Nielson K. (1998) *Animal Physiology: Adaptation and environment*. 5 edn. Cambridge University Press, Cambridge, UK.

Smith D.G. (1985) Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut river system. *Freshwater Invertebrate Biology*, 4, 105-108

Sparks R.E. (1995) Need for Ecosystem Management of Large Rivers and Their Floodplains. *BioScience*, 45, 168-182

Sparks B.L. & Strayer D.L. (1998) Effects of low dissolved oxygen on juvenile Elliptio complanata (Bivalvia:Unionidae). *Journal of the North American Benthological Society*, 17, 129-134

Spooner D.E. (2002) A field experiment examining the effect of freshwater mussels (Unionidae) on sediment ecosystem function. In: *Zoology*, p. 61. University of Oklahoma

Spooner D.E. & Vaughn C.C. (2000) Impact of drought conditions on a mussel bed in the Kiamichi River, southeastern Oklahoma. *Ellipsaria*, 2000, 10-11

Strayer D.L. (1993) Macrohabitats of freshwater mussels (Bivalvia: Unionacea) in streams of the northern Atlantic slope. *Journal of the North American Benthological Society*, 12, 236-246

Strayer D.L. (1999) Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society*, 18, 468-476

Strayer D.L. & Ralley J. (1993) Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society*, 12, 247-258

Strayer D.L., Caraco N.F., Cole J.J., Findley S. & Pace M.L. (1999) Transformation of freshwater ecosystems by bivalves. *BioScience*, 49, 19-27

Strayer D.L., Downing J.A., Haag W.R., King T.L., Layzer J.B., Newton T.J. & Nichols S. (2004) Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience*, 54:429-439.

Strayer D.L., Hunter D.C., Smith L.C. & Borg C.K. (1994) Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. *Freshwater Biology*, 31, 239-248

Suloway L., Suloway J.J. & Herricks E.E. (1981) Changes in the freshwater mussel (Pelecypoda: Unionidae) fauna of the Kaskaskia River, Illinois, with emphasis on the effects of impoundment. *Transactions of the Illinois Academy of Science*, 74, 79-90

Townsend C.R. (1989) The patch dynamic concept of stream community structure. *Journal of the North American Benthological Society*, 8, 36-50

Vannote R.L. & Minshall G.W. (1982) Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Science*, 79, 4103-4107

Vaughn C.C. (1993) Can biogeographic models be used to predict the persistence of mussel populations in rivers? In: *Conservation and Management of Freshwater Mussels: Proceedings of a UMRCC Symposium, 12 - 14 October 1992, St. Louis,MO.* (eds. Cummings KS, Buchanan AC & Koch LM), pp. 117-122. Upper Mississippi River Conservation Commission, Rock Island, Illinois

Vaughn C.C. (1994) Survey for *Arkansia wheeleri* in the Little River. In. U.S. Fish and Wildlife Service, Tulsa, Oklahoma

Vaughn C.C. (1997) Regional patterns of mussel species distributions in North American rivers. *Ecography*, 20, 107-115

Vaughn C.C. (2000) Changes in the mussel fauna of the Red River drainage: 1910 - present. In: *Proceedings of the First Freshwater Mussel Symposium* (eds. Tankersley RA, Warmolts DI, Watters GT, Armitage BJ, Johnson PD & Butler RS), pp. 225-232. Ohio Biological Survey, Columbus, Ohio

Vaughn C.C. (2003a) Biodiversity of freshwater mussel assemblages and their associated macroinvertebrate fauna in streams of the Ouachita Uplands. Final report to National Science Foundation., Washington, D.C.

Vaughn C.C. (2003b) The mussel fauna of the Glover River, Oklahoma. *Proceeding of the Oklahoma Academy of Science*

Vaughn C.C., Pyron M. & Certain D.L. (1993) Habitat use and reproductive biology of *Arkansia wheeleri* in the Kiamichi River, Oklahoma. In. Oklahoma Department of Wildlife Conservation, Oklahoma City

Vaughn C.C., Taylor C.M., Eberhard K.J. & Craig M. (1995) Survey for *Arkansia wheeleri* in eastern Oklahoma and western Arkansas. In. U.S. Fish and Wildlife Service, Tulsa, Oklahoma

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., Mather C.M., Pyron M., Mehlhop P. & Miller E.K. (1996) The current and historical mussel fauna of the Kiamichi River, Oklahoma. *Southwestern Naturalist*, 41, 325-328

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: *Conservation and Management of Freshwater Mussels II: Initiatives for the Future* (eds. Cummings KS, Buchanan AC & Koch LM), pp. 157-162

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. (2000) Macroecology of a host-parasite relationship. *Ecography*, 23, 11-20

Vaughn C.C. & Spooner D.E. (2000) Mussels of the Mountain Fork River. In. USDA Forest Service, Hot Springs, AR

Vaughn C.C. & Hakenkamp C.C. (2001) The functional role of burrowing bivalves in
	freshwater ecosystems. *Freshwater Biology*, 46, 1431-1446.
Vaughn C.C. & Spooner D.E. (2004) Status of the mussel fauna of the Poteau River and
	implications for commercial harvest. *American Midland Naturalist*, 152, 336-346
Vaughn C.C., Gido K.B. & Spooner D.E. (2004a) Ecosystem processes performed by
	unionid mussels in stream mesocosms: species roles and effects of abundance.
	Hydrobiologia, 527, 35-47
Vaughn C.C., Spooner D.E. & Galbraith H.S. (2004b) *Arkansia wheeleri* monitoring in
	the Kiamichi River. In. Oklahoma Department of Wildlife Conservation,
	Oklahoma City
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
Ward J.V. & Stanford J.A. (1987) The ecology of regulated streams: past
	accomplishments and directions for future research. In: *Regulated streams* (eds.
	Craig JFJB & Kemper). Plenum, New York
Watters G.T. (1993) Unionids, fishes, and the species-area curve. *Journal of
	Biogeography*, 19, 481-490
Watters G.T. (1994) *An annotated bibliography of the reproduction and propagation of
	the Unionoidea (primarily of North America). Miscellaneous contributions 1.*
	Ohio Biological Survey.
Watters G.T. (1996) Small dams as barriers to freshwater mussels (Bivalvia, Unionoida)
	and their hosts. *Biological Conservation*, 75, 79-85
Watters G.T. (1999) Freshwater mussels and water quality: a review of the effects of
	hydrologic and instream habitat alterations. In: *Proceedings of the First
	Freshwater Mollusk Conservation Symposium*, pp. 261-274. Ohio Biological
	Survey
Welker, M. & Walz N. (1998) Can mussels control the plankton in rivers? - a
	planktological approach applying a Lagrangian sampling strategy.
	Limn.Oceanogr., 43, 753-762
White D.S. (1977) Changes in the freshwater mussel populations of the Poteau River
	System, Le Flore county, Oklahoma. *Proc. Okla. Acad. Sci.*, 57, 103-105
White D.S. & White S.J. (1977) The effect of reservoir fluctuations on populations of
	Corbicula manilensis (Pelecypoda: Corbiculidae). *Proceedings of the Oklahoma
	Academy of Sciences*, 57, 106-109
Williams C.J. & McMahon R.F. (1985) Seasonal variation in oxygen consumption rates,
	nitrogen excretion rates and tissue organic carbon:nitrogen ratios in the introduced
	Asian freshwater bivalve, *Corbicula fluminea* (Muller) (Lamellibranchia:
	Corbiculacea). *American Malacological Bulletin*, 3, 267-269
Williams J.D., Fuller S.L.H. & Grace R. (1992a) Effects of impoundments on freshwater
	mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black
	Warrior and Tombigbee Rivers in western Alabama. *Bulletin of the Alabama
	Museum of natural History*, 13, 1-10
Williams J.D., Warren M.L., Jr., Cummings K.S., Harris J.L. & Neves R.J. (1992b)
	Conservation Status of Freshwater Mussels of the United States and Canada.
	Fisheries, 18, 6-22

Wyckoff D.G. (1976) Faunal materials from four early Caddoan tradition sites, Arkansas Basin, eastern Oklahoma. In. University of Oklahoma Department of Archaeology, Norman

Yeager B.L. (1993) Dams. In: *Impacts on warmwater streams: guidelines for evaluation*, pp. 57-113. Southern Division, American Fisheries Society, Little Rock, Arkansas

Yeager M.M., Cherry D.S. & Neves R.J. (1994) Feeding and burrowing behaviors of juvenile rainbow mussels, *Villosa iris* (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, 13, 217-222

Young M. & Williams J. (1983) The status and conservation of the freshwater pearl mussel *Margaritifera margaritifera* Linn. in Great Britain. *Biological Conservation*, 25, 35-52