FINAL PERFORMANCE REPORT

FEDERAL AID GRANT NO. T-38-P-1

SURVEYS FOR RARE MUSSEL SPECIES AND DETERMINATION OF HYDROLOGICAL CHARACTERISTICS OF MUSSEL HABITAT IN SOUTHEAST OKLAHOMA

OKLAHOMA DEPARTMENT OF WILDLIFE CONSERVATION

June 1, 2006 through May 31, 2008

FINAL PERFORMANCE REPORT

State: Oklahoma **Grant Number:** T-38-P-1

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Grant Title: Surveys for Rare Mussel Species and Determination of Hydrological Characteristics of Mussel Habitat in Southeast Oklahoma

Grant Period: June 1, 2006 – May 31, 2008

Principal Investigator: Dr. Caryn C. Vaughn

Objective:

(1) Conduct surveys for rare freshwater mussel species in the Little River, Oklahoma.

(2) Measure and estimate complex hydraulic conditions of mussel sites in the Little River to determine how these parameters can be used to characterize rare mussel species habitat.

(3) Conduct experiments to determine how common freshwater mussel species modify habitat, making it appropriate for rare freshwater mussel species.

Need:

Rare mussels in southeastern Oklahoma and need for status surveys

Freshwater mussels are one of the most threatened faunas globally due to habitat destruction and alteration, population fragmentation, and introduction of non-native species (Strayer et al. 2004). Freshwater mussel populations in southeastern Oklahoma are no exception. There are 19 species identified as Species in Greatest Conservation Need that are known from the Kiamichi and Little River watersheds (Spooner et al. 2005, Vaughn 2005). These include 9 Tier I species: Ouachita Rock Pocketbook *(Arkansia wheeleri),* Scaleshell *(Leptodea leptodon)*, Ouachita kidneyshell *(Ptychobranchus*

occidentalis), Rabbitsfoot *(Quadrula cylindrica)*, Ouachita Creekshell *(Villosa arkansasensis)*, Butterfly *(Ellipsaria lineolata)*, Southern Hickorynut *(Obovaria jacksonia)*, Winged Mapleleaf *(Quadrula fragosa), and* Purple Lilliput *(Toxolasma lividum)*; 5 Tier II species: Plain pocketbook *(Lampsilis cardium)*, Louisiana fatmucket *(Lampsilis hydiana)*, Ohio River Pigtoe *(Pleurobema cordatum)*, Wartyback Mussel *(Quadrula nodulata)*, and Texas Lilliput *(Toxolasma texasensis)*; and 5 Tier III species: Threeridge Mussel *(Amblema plicata)*, Washboard *(Megalonaias nervosa)*, Bluefer *(Potamilus purpuratus)*, Monkeyface Mussel *(Quadrula metanevra)*, and Little Spectaclecase *(Villosa lienosa)*. Three of these species are listed as federally endangered, the Ouachita Rock Pocketbook, Scaleshell and Winged Mapleleaf, and the Rabbitsfoot have been proposed for listing.

Mussels in southeastern Oklahoma are declining (Vaughn and Taylor 1999, Vaughn 2000, Galbraith et al. 2005, 2008) and are threatened by land use changes, particularly by proposed plans to divert water from Oklahoma rivers to Texas. It is critical that the status of mussel populations in these rivers, particularly Tier I species, be assessed before decisions regarding water transfers/diversions are made. Mussel populations in the Kiamichi River were assessed from 2003 – 05 (Galbraith et al. 2005, 2008) and, because of some supplemental funding, we were able to sample five sites in the Little River during this time period (Galbraith et al. 2005, 2008). In this survey of the Little River we found what were confirmed to be live individuals of *Quadrula fragosa* at 4 sites, *Arkansia wheeleri* at one site, and *Quadrula cylindrica* at four sites. The *Q. cylindrica* populations that we found are believed to be some of the healthiest in the world (Butler 2005, Galbraith et al. 2005).

Quantification of habitat requirements for rare mussel species

Mussels are naturally patchily distributed in rivers, often occurring in densely aggregated multi-species "beds" separated by areas where mussels occur sporadically or not at all (Vaughn and Pyron 1995, Strayer et al. 2004, Strayer 2008). The patchy distribution of these mussel beds has intrigued malacologists for some time, but investigations into habitat requirements for mussel beds have largely failed to predict their distribution based on environmental variables such as depth, current velocity, substrate composition (sand vs. gravel, etc.), food availability, particulate organic carbon, calcium concentration, or stream gradient (Strayer 1993, Strayer and Ralley 1993, Strayer et al. 1994). We know that stream flow patterns are important to mussels, but conventional methods for estimating instream flow preferences for mussels have been largely unsuccessful (Gore et al. 2001). For example, Layzer and 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 as depth and velocity, complex hydraulic characteristics such as shear stress, an indicator of near-bed flow, have been shown to be significantly correlated with mussel abundance and the occurrence of mussel beds (Layzer and Madison 1995, Howard and Cuffey 2003, Gangloff and Feminella 2007). These areas with low shear stress during floods are not as

susceptible to bed scouring, which is a major cause of freshwater mussel mortality during floods (Hastie et al. 2001). Strayer (1999) found that mussel beds were located in areas protected from high flows and subsequent substrate movement. Thus, at the stream reach scale and larger (macrohabitat), the occurrence of mussel habitat is likely governed by interactions between geomorphology and hydrology, and mussels are most likely to be successful in areas that remain free-flowing and oxygenated during the summer low-flow periods but that are protected from shear stress during high water periods.

In many cases, 'rare' mussel species are only found in the largest, most species-rich mussel beds. This has been documented for *Arkansia wheeleri* (Vaughn and Pyron 1995) and we think this also may be true for *Quadrula fragosa.* While surveying for *A. wheeleri* in the Little River, Galbraith et al. (2005) discovered live individuals of *Q. fragosa.* These individuals were restricted to large, species-rich beds. Why do rare mussel species only occur in the presence of other mussels (i.e. within the largest and most species-rich mussel beds)? One hypothesis for this phenomenon is that mussels themselves, by the presence of their shells and through their burrowing activities, stabilize streambed sediments, decrease shear stress, and thus create more appropriate microhabitat for other mussel species (Vaughn and Hakenkamp 2001). For example, Hardison and Layzer (2001) found that shear velocity varies on a small spatial scale within mussel beds and is negatively correlated with mussel density. Substrate (river bed sediments) stability has been suggested to be an important factor contributing to freshwater mussel habitat (Vannote and Minshall 1982, Strayer and Ralley 1991). During floods, bed-load movement of sediments has the potential to dislodge and displace freshwater mussels in areas where the substrate is not stable, and consequently

stable substrate has been found to be an important contributor to suitable freshwater mussel habitat (Strayer 1999, Johnson and Brown 2000). However, there has not been research investigating whether freshwater mussels themselves contribute to substrate stability. Burrowed freshwater mussel biomass can dominate the substrate, for example in the Little River we have found up to 20 kg/m^2 of freshwater mussels (Spooner, unpub.), and these large, thick shelled animals are likely to stabilize the substrate. We think that large numbers of common freshwater mussel species in a mussel bed may stabilize the riverbed and facilitate the recruitment of rare freshwater species.

Being able to quantify and predict where appropriate mussel habitat occurs in rivers in southeastern Oklahoma, and understanding how mussels themselves may modify habitat and make it more appropriate for rarer mussel species, are critical conservation needs in this region. The major cause of mussel decline in the U.S. is from the alteration of the natural flow regime of rivers (Vaughn and Taylor 1999, Watters 2000, Strayer et al. 2004). Mussel populations in southeastern Oklahoma currently are threatened by proposed plans to sell water from the Little and Kiamichi rivers. If these plans are carried out, water may be diverted from the Little River, its tributary the Mountain Fork River, and from the nearby Kiamichi River. These actions may impact the mussel populations in these rivers, by altering stream hydrology and the subsequent creation of new mussel habitat. Additionally, both of these rivers are already impounded; current patterns of water release may already be influencing their habitat.

The goals of the proposed work are to assess the status of rare freshwater mussel species in the Little River, Oklahoma, and determine the hydrological habitat

characteristics for rare freshwater mussel species, to help inform state and federal management agencies and to identify and address mussel conservation needs.

Methods:

I. STATUS SURVEYS FOR RARE MUSSEL SPECIES

In July of 2006, we conducted a survey of the Little River for rare mussel species. Because Galbraith et al. (2008) first documented the occurrence of the Federally Endangered Winged Mapleleaf, *Quadrula fragosa*, at three sites on the Little River, we focused our survey to document the extent of this species. Because Vaughn and Taylor (1999) previously described mussel communities of the Little River, we decided to focus our efforts on a section of the Little River between the Wright City Bridge and the confluence of the Little and Mountain Fork Rivers. Vaughn and Taylor (1999) observed the most diverse mussel beds in this section of the river, therefore we suspected that the range of *Q. fragosa* populations would lie within this section of river.

We surveyed a total of 19 sites (Fig. 1), conducting qualitative timed surveys at 17 of these sites and quantitative quadrat surveys at 6 of these sites. Timed surveys consisted of the collection of live mussels and spent shells by feeling and grubbing through the river bottom at a site for 1-2 person-hours. All mussels and shells collected were identified to species, and live mussels were measured for length. Quadrat surveys consisted of placing 24, 0.25 m^2 quadrats throughout a mussel bed, and excavating the quadrat for exposed and buried mussels. To place the quadrats, we delineated 6 transects across the river bed that were equally spaced 10-20 m apart, depending on the size of the mussel bed. Each transect was permanently marked on the bank by marking trees.

Along each transect, we placed 4 quadrats at regular intervals across the transect. All mussels and spent mussel shells collected within a quadrat were identified to species and live mussels were measured for length.

II. QUANTIFICATION OF HABITAT REQUIREMENTS FOR RARE MUSSEL SPECIES

We conducted a field study investigating if substrate and hydraulic characteristics can be used to predict the occurrence of mussels, and if they can be used to predict the occurrence of rare freshwater mussel species. For this study, we used the six field sites where we took quadrat samples (Sites 9-10,16-19). At each quadrat, we filled a 0.72 L plastic bag with a sample of the armored layer of substrate. Substrate samples were taken back to the lab, dried for 48 hrs at 100°C, sieved through a series of 12 geological sieves (sizes in mm: 63.5, 38.1, 19, 8, 3.962, 1.981, 0.991, 0.495, 0.246, 0.175, 0.088, and 0.061) and weighed. We took flow measurements to model hydraulic characteristics at two flow levels; once during summer 2006 low-flow season, and once again during fall 2006-spring 2007 when flow levels were higher. Additionally, at each site we measured water depth and current velocity at the center of 1 m cells along a cross-section of the river for discharge calculations. Flow measurements consisted of measuring the slope of the waterline with a surveyor's level, measuring water depth using a meter-stick or a Hondex™ digital depth sounder if depth > 1 meter, and water velocity at 0.6 d using a Marsh-McBirney™ Flo-Mate flow-meter. At high flows, we were unable to measure the slope of the water line due to high flow conditions, so we substituted our slope measurements at low flow when modeling hydraulic parameters at high flows.

Substrate and hydraulic parameters were calculated using formulae in Table 1. To quantify the relative flow levels that our data represent, we calculated quantile exceedance levels of our calculated discharge relative to historical data collected from a USGS gauging station (1946-2007, station #07338500, USGS) just downstream of site 17 (Fig. 1).

Statistical analysis: Discriminant function analysis (DFA) is a statistical method that uses multivariate data to generate a single function that can be used to determine how well data points are classified into different groups (Sokal and Rohlf 1995). We used DFA to test three hypotheses: 1) that substrate and hydraulic data can be used to predict the presence and absence of mussels, 2) that substrate and hydraulic data can be used to predict the presence and absence of rare mussel species, and 3) that hydraulic parameters modeled at high flows would better predict the presence of mussels or rare mussel species better than hydraulic variables modeled at low flows. We first classified our data as either having mussels present (n=136) or absent (n=8), and ran DFA twice; once using hydraulic parameters modeled at low flows, and once using hydraulic parameters modeled at high flows. To determine the accuracy of our DFA models, we "trained" our DFA model with a random subset of 94 data points, and used the remaining 50 data points to determine the percent accuracy of our trained DFA model. Second, we classified our data as either having rare mussel species present or absent, and then ran DFA as above. To classify a quadrat as having a rare species present, we *a priori* classified a rare mussel species as a species having less than 2% relative abundance at a given site, which gave us an even split of quadrats with rare species present (n=72) or absent (n=72).

III. HABITAT MODIFICATION BY COMMON MUSSEL SPECIES

Because the results of part II suggested that rare mussel species are more likely to occur where substrates are more stable, we conducted an experiment to see if common freshwater mussel themselves stabilize substrates, improving habitat for rare mussel species.

Experimental Units: Experiments investigating how organisms influence substrate stability in natural settings are uncommon because of the difficulty of controlling physical factors important to bed stability, such as substrate composition and flow characteristics. However, many authors have had success using experimental channels that can control hydrodynamic and substrate properties (Vogel and LaBarbera 1978, Nowell and Jumars 1987, Cardinale et al. 2004). We constructed a set of eight recirculating stream channels ("flumes") modeled after the design of Vogel and LaBarbera (1978) so that we could isolate the effects of freshwater mussels on substrate stability. The channel in each flume was 0.33m × 0.33m × 3.30m, each with a 0.11 m^2 working section located 2.64 m downstream of the flow entrance (8× the channel width, as recommended by Nowell and Jumars (1987)).

Experimental Treatments: We designed an experiment to investigate how mussel density and mussel community diversity influenced substrate stability. We collected individuals of three common mussel species from a single site in the Kiamichi River in southeast Oklahoma (*A. ligamentina* n=79, *A. plicata* n=83, *Q. pustulosa* n=80). These mussels were randomly assigned to one of eight diversity treatments per trial (one per flume). Diversity treatments were composed of three monocultures (solely one of the three species), three treatments of all possible combinations of two species, one three

species treatment, and a no mussel control. We crossed each diversity treatment with two density treatments to generate a factorial design by randomly selecting a trial to be run at one of the two density treatments (6 mussels, ~55 mussels/m^2; and 12 mussels, ~110 mussels/m^2). In total we ran 24 trials, so that each diversity treatment was replicated for density treatment 12 times. Diversity treatments were assigned to a flume and a randomized-block design such that each diversity treatment was run in each flume at least twice.

Methods: Each working section was filled with 4.01 L of a homogenized gravel mixture typical of mussel beds in southeast Oklahoma. We measured the volume of water displaced by the mussels to be added so that we could remove the corresponding volume of gravel that would be displaced by mussels as they burrow. Because these mussel species vary in burrowing depth (Allen and Vaughn 2009), we corrected the volume of gravel removed by the mean proportion of the mussel that is buried beneath the sediment from a previous study (*A. ligamentina* = 0.74, *A. plicata* = 0.75, *Q. pustulosa* = 0.90; (Allen and Vaughn 2008, Allen, unpub.)) Mussels were placed into the working sections in one of 16 random locations on a grid placed on top of the substrate, which was subsequently removed. Following the addition of mussels, we filled the flume to a depth of 33 cm and set the flow velocity at 5 cm/s. At these ambient conditions, we estimated Reynolds number to be 16,510 and Froude number to be 0.03. Mussels were given two days to burrow into the substrate before a trial began.

For each trial we recorded water temperature, photographed the working section to record the position of the mussels, and measured the height, width, and length of all exposed portions of mussels. Then we increased the flow velocity of each flume to

maximum speed (mean ± SE (cm/s) = 83 ± 0.42) for two minutes during which all eroded substrate was caught in a net downstream of the working section. At these peak flow conditions, we estimated Reynolds number to be 274,066 and Froude number to be 0.46. This time period was chosen because pilot studies showed that all possible substrate movement occurred in the first two minutes. After the trial, the eroded gravel was dried for 48 h at 100°C and weighed.

Statistical Analysis: We hypothesized that mussels would have stabilizing and destabilizing effects on substrate depending on mussel species, and that these effects would be greater at higher mussel densities. To test the hypothesis that freshwater mussels influence substrate stability, we performed several quantile regressions on log (x + 1) transformed gravel eroded (g) with mussel density as the independent variable. To test the hypothesis that mussel diversity would influence substrate stability, we also ran this analysis again using mussel species richness as the independent variable. Because of a clear violation of heteroscedacity, traditional least means squared regressions were inappropriate for our data (Figs. 4-5). Quantile regression is a statistical method used in ecological studies, and does not assume equal variances along the axis of the independent variable (Cade and Noon 2003, Koenker 2005). To explore the general effect of mussels, we modeled the 50th quantile regression line, and to quantify the stabilizing and destabilizing effects of mussels we modeled the 5th, 10th, 25th, 75th, 90th, and 95th quantile regression lines. To model quantile regression lines, we used the "quantreg" package developed for R© software (Koenker 2008).

Because treatment species richness had a positive effect on destabilization, we hypothesized that effects of mussel diversity treatments on substrate stability would vary.

To test this hypothesis, we ran a one-way ANOVA on eroded gravel (g) relative to no mussel treatments using diversity treatment as a factor. Because of the presence of outliers in our dataset (Fig. 6), we used 20% trimmed means and 20% Winsorized variances in ANOVA computations to make our analysis more robust to outliers (Wilcox 2003). Additionally, we ran two sets of post-hoc contrasts to test two hypotheses. First, we ran contrasts amongst all monocultures to test for differences between monocultures. Second, we wanted to test the null hypothesis that the performance of a multiple species treatment could be predicted additively by monocultures, and we ran a set of post-hoc linear contrasts comparing multi-species treatments its corresponding monocultures. All post-hoc contrasts used 20% trimmed means and 20% Winsorized variances, and the Welch-Sidak method to control for Type I errors (Wilcox 2003).

Results:

I. STATUS SURVEYS OF RARE MUSSEL SPECIES

The results from our timed and quadrat surveys are given in Tables 2 and 3, respectively. Mussels were present at all survey sites, and all sites had diverse mussel communities (species richness ≥ 9 for all sites). In total we found 25 species of mussels in our study section of the Little River, 9 of which are considered species of greatest conservation need (Spooner et al. 2005, Vaughn 2005). We found five Tier I species: butterfly (*Ellipsaria lineolata*) at 8 sites, southern hickory nut (*Obovaria jacksonia*) at 13 sites, Ouachita kidney shell (*Ptychobranchus occidentalis*) at 8 sites, rabbitsfoot (*Quadrula cylindrica*) at 15 sites, and winged mapleleaf (*Quadrula fragosa*) at 7 sites; one Tier II species: fat pocketbook (*Lampsilis cardium*) at 14 sites; and three Tier III

species: three ridge (*Amblema plicata*) at all 19 sites, washboard (*Megalonaias nervosa*) at 15 sites, and bluefer (*Potamilus purpuratus*) at 11 sites. Of these species, the winged mapleleaf (*Q. fragosa*) is federally endangered, and the rabbitsfoot (*Q. cylindrica*) is a species of special concern in Oklahoma (Galbraith et al. 2008). Notably absent from our survey is any record of the federally endangered Ouachita rockpocketbook (*Arkansia wheeleri*).

II. QUANTIFICATION OF HABITAT REQUIREMENTS FOR RARE MUSSEL SPECIES

The results from our discriminant function analyses are summarized in Tables 4-5 and Figures 2-3. Discriminant function models (DFM) were able to successfully predict the presence or absence of mussels well using substrate and hydraulic variables. At low flows, the DFM successfully predicted the presence or absence of mussels 96% of the time. The low flow DFM was most influenced by D S.D. (substrate heterogeneity) and then τ_* (substrate movement), as quadrats with mussels present had more homogenous substrate and, interestingly, more substrate movement at low flows (Table 4). The high flow DFM performed even better than our low flow DFM, successfully predicting the presence or absence of mussels 100% of the time. Similar to our low flow DFM, our high flow DFM was most influenced by τ_* and D S.D.; with the clear distinctions being that quadrats with mussels present had lower substrate movement at high flows, and that the influence of substrate stability was much stronger than substrate heterogeneity (Table 4). Overall our DFM separated the quadrats with mussels present or absent very well, as

their distributions were very different along the discriminant function score axis (Figure 2).

Our DFM had less success predicting the presence or absence of rare mussel species. At low flows, our DFM performed very poorly, and did not successfully predict the presence or absence of mussels any better than random chance could, as it only predicted the presence of rare mussel species 48% of the time (Table 5). Indeed, the distributions of quadrats with rare versus common mussel species showed no differences along the discriminant function score axis (Fig. 3). However, at high flows our DFM were better at predicting the occurrence of rare mussel species, with a 60% success rate. The high flow DFM model was driven by τ_*, as quadrats with rare mussel species present had lower substrate movement than those with only common species present (Table 5). Overall, the distribution of quadrats with rare species present peaked at higher discriminant function scores than quadrats with only common species present (Fig. 3).

III. HABITAT MODIFICATION BY COMMON MUSSEL SPECIES

Summaries of our quantile regression (QR) models for eroded gravel using mussel density and diversity as independent variables are given in Tables 5-6, and shown in Figures 4-5. For mussel density, the 50th QR model was not significant, suggesting that mussel density does not influence substrate stability. However, the 90th, 75th, and 5th QR were significant. This suggests that mussels can have a destabilizing effect on substrates (90th and 75th QR models) as well as a stabilizing effect (5th QR model), that cancel each other out so that there is no overall effect of mussel density on substrate stability. For species richness, the 50th QR model was significant with positive

coefficients, suggesting that increased the mussel diversity in a treatment has a destabilizing effect on mussels, a point reinforced by the significant 75th QR model.

The results of our ANOVA on gravel eroded (g) relative to control treatments using 20% trimmed means and 20% Winsorized variances showed a significant effect of diversity treatment ($F_{6,46.51}$=3.27, p=0.009). Interestingly, post-hoc tests showed no significant difference between monocultures, and a significant difference between the performance of the 3 species treatment and the expected value of additive effects of monocultures (Fig. 6). Although post-hoc contrasts showed no significant difference between monocultures, *A. ligamentina* had a strong destabilizing effect relative to the no mussel control, and *A. plicata* and *Q. pustulosa* had slight destabilizing and stabilizing effects relative to controls (20% trimmed means of gravel eroded relative to control (g): *A. ligamentina*, 35.6; *A. plicata* 2.1; *Q. pustulosa:* -2.0; Fig. 6).

Conclusions and Recommendations:

I. STATUS SURVEYS OF RARE MUSSEL SPECIES

Tier I Species: Our survey expanded on the known range of the federally endangered *Q. fragosa*, winged mapleleaf, in the Little River. Galbraith et al. (2008) first recorded live individuals of *Q. fragosa* at four sites from the Little River, including three sites surveyed in this study. Galbraith et al. (2008) found *Q. fragosa* at sites 11, 16, and 18 covered in our survey; in addition to a site located just upstream of the confluence of the Mountain Fork and Little Rivers (Fig. 1). In addition to these sites, we found live *Q. fragosa* individuals at sites 9-10, 12-14, 17 and 19 (Tables 2-3); thus, there are 11 sites on the Little River where live *Q. fragosa* individuals have been found between the Galbraith

et al. (2008) survey and ours. Interestingly, we did not find *Q. fragosa* at any of the three Galbraith et al. (2008) sites we went to. Because *Q. fragosa* is a very rare mussel, a site where it is present could easily be surveyed without it being found. That makes it very likely that *Q. fragosa* occurs at more sites, even ones we have already surveyed. Thus, *Q. fragosa* likely exists at any dense, speciose mussel bed on the Little River from around site 9 downstream to the confluence of the Mountain Fork River. However, there is a gap in our survey coverage downstream site 19 to the confluence of the Mountain Fork, so we recommend additional surveys in the future to see if *Q. fragosa* occurs there.

Because of the impact the cold-water releases from Broken Bow Lake to the Mountain Fork, mussel species richness in the Little River declines drastically after the confluence of the Mountain Fork River (Vaughn and Taylor 1999). Therefore, it is unlikely that the range of *Q. fragosa* in the Oklahoma portion of the Little River extends beyond the confluence of the Mountain Fork River. Overall, we think that the Little River in OK may have some of the most abundant populations of *Q. fragosa* in the world, and recommend that all possible steps be taken to protect these populations. Additionally, if the Broken Bow Lake dam were able to adapt their releases to be from both the top and bottom parts of the lake (so that the releases would have higher summer temperatures), we think that mussel habitat in the Little River below the confluence of the Mountain Fork would be improved, and that the range of *Q. fragosa* may eventually extend downstream in the Little River.

Other Tier I species found in our survey include *Quadrula cylindrica, Obovaria jacksonia,* and *Ellipsaria lineolata*. We found that *Q. cylindrica* had a very broad range in the surveyed portion of the Little River (Tables 2-3), which confirms previous

descriptions of the Little River possibly harboring the most abundant populations of *Q. cylindrica* in the world (Galbraith et al. 2008). Like *Q. cylindrica, O. jacksonia* also had a broad range in our survey, although it was not very abundant. Like *Quadrula fragosa, E. lineolata* was present in the lower portion of the surveyed range of the Little River, where mussel beds were denser and speciose, and was not very abundant.

One Tier I species that was notably absent in our survey was the federally endangered *Arkansia wheeleri*, which is known from the Little River. This species was found in the 1990s at two of the sites we surveyed for this project (Vaughn and Taylor 1999). Although *A. wheeleri* was recently found at a site just upstream of the confluence of the Little and Mountain Fork rivers (Galbraith et al. 2008), we are concerned about the status of *A. wheeleri* in the Little River.

Tier II Species: The only Tier II species found in our survey was *Lampsilis cardium,* and it was present at many of our sites and showed a broad range within our survey (Tables 2-3, Fig. 1). However, *L. cardium* was not very abundant, as we only found very few individuals where it was present.

Tier III Species: We found three Tier III species in our survey, *Amblema plicata, Megalonaias nervosa,* and *Potamilus purpuratus*. We found very abundant populations of *A. plicata*, as it was present at every site and was one of the most common species in the Little River (Fig. 1, Tables 2-3). We also found moderately abundant populations of *M. nervosa,* which also had a broad range in our survey (Fig. 1, Tables 2-3). However, these two species are the most common targeted species by mussel harvesters due to their thick shell that is desired for their use in the pearl culture industry. Because rare mussel species (such as *Quadrula fragosa* and *Arkansia wheeleri*) are only found in the most

dense mussel beds (Vaughn and Pyron 1995, Hornbach et al. 1996), we believe that common mussel species play important roles in modifying habitats to make them more suitable for mussel species. Therefore, although the populations of *A. plicata* and *M. nervosa* are abundant on the Little River, we recommend that the Little River be established as a mussel harvesting sanctuary to protect the many rare mussel species that occur there.

II. QUANTIFICATION OF HABITAT REQUIREMENTS FOR RARE MUSSEL SPECIES

Presence and Absence of Mussels: Our discriminant function models (DFMs) using substrate and hydraulic parameters performed very well at predicting the presence or absence of mussels at low and high flows, with prediction successes of 96% and 100%, respectively. Both the low and high flow DFMs had high coefficients for substrate heterogeneity (D. S.D.), and for modeled substrate movement (τ_*). For both flow levels, our DFMs had strong negative coefficients for substrate heterogeneity, meaning the mussels were more likely to be present where substrates were less heterogenous. At first glance this finding may be counterintuitive, as heterogeneous substrates are often associated with higher abundances of other stream organisms, such as benthic macroinvertebrates (Allan and Castillo 2007). One might suspect that an increase in substrate heterogeneity could provide different habitat types for juvenile and adult mussels, since juvenile mussels have been documented to prefer different habitats than adults (Neves and Widlak 1987). Upon closer inspection, we found that in our study, substrate heterogeneity was most strongly correlated with substrate movement modeled at

high flows (r=0.42). This suggests that quadrats with homogenous substrates were also associated with quadrats that were more stable during high flows. Many authors suggest that substrate stability at high flows is an important factor regulating the distribution of mussels (Strayer 1999, Morales et al. 2006, Strayer 2008). Therefore, some of the importance of substrate heterogeneity in our DFMs may be indirectly related to the importance of substrate stability at high flows.

Interestingly, there was a sign difference for our coefficients for modeled substrate movement (τ_*) in the low and high flow DFMs for presence and absence of mussels. At low flows, the coefficient for τ_* was positive, while at high flows it was negative. On the one hand, this coincides with previous studies suggesting mussel abundance is negatively associated with substrate movement at high flows (Strayer 1999). However, to our knowledge, a positive association between mussel presence and substrate movement at low flows has not been reported. Because freshwater mussels are largely sessile, they are thought to be very sensitive to sedimentation; or the deposition of fine sediments where they occur (Box and Mossa 1999). Therefore, mussels may be more likely found in areas where sedimentation is not occurring, i.e. areas where fine sediments are constantly swept away, even at low flows. Because at low flows the flows are not strong enough to scour gravel, cobble, or mussels; this may explain why we found a positive association of modeled substrate movement at low flows and mussel presence. Additionally, mussels likely need some flow in order to bring them suspended food particles to feed on.

Surprisingly, our results contradict the results of previous studies suggesting that mussels are present or more abundant at areas with lower shear stresses (Hardison and

Layzer 2001, Howard and Cuffey 2003, Gangloff and Feminella 2007). In our study, quadrats with mussels present had higher shear stresses at higher flows than quadrats with mussels absent (Table 5). However, these authors all suggested that areas with higher shear stresses were more likely to have substrate movement, which is why they found mussels in areas of low shear stress (Hardison and Layzer 2001, Howard and Cuffey 2003, Gangloff and Feminella 2007). Interestingly, our interpretation of our results comes to the same conclusion, as quadrats with mussels present had lower values for Shield's entrainment function (τ_*), which models substrate movement. This suggests that the substrate size is more important to substrate stability than shear stress in the Little River, since τ_* uses a measure of substrate size in addition to near-bed flow velocity to model substrate movement.

Presence of Rare Mussel Species: Our DFMs using substrate and hydraulic parameters to predict the presence of rare mussel species did not perform as well as our DFMs predicting the presence or absence of mussels. At low flows, our DFM was only successful at predicting the presence of a rare mussel species 48% of the time, which is no better than a random probability of 50%. To a certain extent this was expected, since hydraulic forces at high flows have been suggested to be more important factors for freshwater mussel habitat than the same forces at low flows (Layzer and Madison 1995, Howard and Cuffey 2003, Zigler et al. 2008). If the presence of rare mussel species is a function of habitat quality as measured by hydraulic forces, then we would not expect our DFM to be able to predict rare species presence using low flow hydraulic parameters. However, given the success of our low flow DFM to predict the presence or absence

mussels (96%), we were surprised that the low flow DFM did not predict the presence of rare mussel species any better than random chance.

Our high flow DFM performed better at predicting the presence of rare mussel species, with 60% success rate. The strongest coefficient in this DFM was modeled substrate movement (Table 5), followed by substrate heterogeneity. This analysis suggests that rare species are more likely to occur in areas that are more stable during high flows. However, overall the prediction power of this DFM is not very high, but is better than random chance. We think that this means that substrate stability is an important factor in habitat requirements for rare species, but that there are other unmeasured factors aside from hydraulic parameters and substrate characteristics that are also important. Because many mussel species have specific fish host requirements (which is partly responsible for freshwater mussel diversification), fish species richness and fish host abundances are also very likely to be an important factor for rare mussel species habitat that was unmeasured in this study (Vaughn and Taylor 2000, Barnhart et al. 2008, Strayer 2008). Other factors likely to be important include water quality, food quality, and food quantity (Strayer et al. 2004, Strayer 2008). Therefore, future investigations into the habitat requirements for rare mussel species should take a multi-factor approach to include factors unmeasured in this study to predict the presence and abundance of rare mussel species.

Overall, we found that hydraulic and substrate parameters, particularly modeled substrate movement and substrate heterogeneity, are important factors for mussel habitat. Using discriminant function analysis, we were able to use these parameters to successfully predict the presence or absence of mussels, at both high and low flow levels.

However, these parameters were less successful at predicting the presence of rare mussel species, especially at low flows. Because of the presence of impoundments in the Little River watershed, we recommend that natural resource managers and the Army Corp of Engineers to work together to establish flow regimes that promote substrate stability and avoid sedimentation, but still allow for the recreational and flood control benefits of dams.

III. HABITAT MODIFICATION BY COMMON MUSSEL SPECIES

Our quantile regression models showed that mussel density has both stabilizing and destabilizing effects on substrate, and that these effects are stronger at higher mussel densities (Fig. 4). These results contradict the hypotheses of several authors that mussels stabilize substrates during high flow events (Zimmerman and de Szalay 2007, Strayer 2008). Furthermore, a previous laboratory investigation showed that two species of mussels had no effect on substrate erosion (including *Actinonaias ligamentina*, a species used in our study) although mussels made sediments more cohesive over the course of four weeks (Zimmerman and de Szalay 2007). Each trial of our experiment only lasted four days, so any influence mussels have on increasing sediment cohesion over such a long period of time would not have been able to occur in our experiment.

Mussel diversity was at least partly responsible for the effects of mussels on substrate stability. Quantile regression models showed that mussel species richness had a destabilizing effect on substrate (Fig. 4). Additionally, we found that there were significant differences between mussel diversity treatments, suggesting that the effects of mussel species, and combinations of mussel species differed (Fig. 6). Interestingly, the

three species treatment had a stronger destabilizing effect than would have been predicted by the performance of the monocultures, suggesting a complementary interaction between the species.

The effect of mussels on substrate stability is likely to be strongly influenced by body size, burrowing position and behavior, and shell morphology. All of these factors are likely to influence near-bed hydraulics, which are ultimately responsible for the erosion of substrate. The three mussel species varied in size, with *A. ligamentina* being the largest, *Q. pustulosa* being the smallest, and *A. plicata* being medium sized. Body size is likely to be important because when an object projects from the sediment-water interface, wake and vortices are formed downstream of the object, which can cause erosion of substrate (Vogel 1994). Additionally, the burrowing position of the mussel (how much of its body is exposed to the water) will also be important. Of the species in this study, *A. ligamentina* is and *A. plicata* are more epibenthic than *Q. pustulosa* (Allen and Vaughn 2009, Allen unpub.). Likewise, the angle of the shell relative to the will be important, because if the mussel is aligned parallel to flow direction, it will be more hydrodynamic, cause less drag, and less wake will form behind the mussel (Vogel 1994). Burrowing activity will also be important, as the more active a burrower species is, the more likely that it will disrupt sediments via bioturbation, decreasing sediment cohesion and increasing susceptibility to erosion.

Shell morphology will also be important, as the shell sculpturing will also influence how much wake is formed. Of the species used in our study, *A. ligamentina* is smooth shelled, *A. plicata* is ridged, and *Q. pustulosa* has pustules. Mussel species are thought to have evolved to have shell sculpturing to prevent scour, as shells with ridges

or pustules generate a larger number of smaller vortices in random directions (which can both destabilize and stabilize nearby sediments), whereas species with smooth shells will generate fewer larger vortices in predominantly destabilizing directions (Watters 1994). This phenomenon operates on the same principle that allows a dimpled golf ball to travel farther than a perfectly smooth golf ball (Vogel 1994).

Therefore, *A. ligamentina* is likely to have predominantly destabilizing effects because it is a large, epibenthic mussel that burrows actively and has a smooth shell. *A. plicata* has a slight destabilizing effect on substrate stability because while it is of medium size and an inactive burrower (Allen and Vaughn 2009), its ridges help to prevent scour (Watters 1994). *Q. pustulosa* has a slight stabilizing effect because of its small size, deeper burrowing position, and pustules. However, mussels rarely occur as a single species in nature, they almost always occur as multi-species assemblages. Our diversity treatments that were composed of different species combinations were meant to reflect how mussels occur in nature to make our results more applicable to the real world. Therefore, it is interesting that while most of our multi-species treatments could be predicted additively from the performance of monocultures, our three species treatment did not – destabilizing substrates significantly more than would be expected. Because the three mussel species differ so much in size, shell morphology, and burrowing behavior, it is very likely that the three species treatment generated the most topographically complex sediment-water interface, generating more turbulence and erosion.

While our experiment yielded some interesting results, it is not without limitations. Zimmerman and de Szalay (2007) found that mussels decreased sediment cohesion within the first week, presumably as mussels buried and positioned themselves

into the sediment. Because we ran the substrate stability trials so soon after the addition of mussels, this fact may have biased our experiment towards destabilizing effects. However, we also had biases towards stabilizing effects due to our methods of calculating how much gravel to remove from the working section when mussels were added. We removed an amount of gravel that displaced a certain volume of water. This volume of water was calculated based on the volume of water displaced by the mussels to be added, and then corrected by a factor based on the species' burrowing behavior (how deep the species tends to burrow within the sediment). However, the volume of water displaced by gravel is much less than the volume of space that same amount of gravel occupies—this is due to the fact that gravel particles have spaces between them—interstitial pores. Because our experiment may have biases towards both stabilizing and destabilizing effects, they are likely to account for each other to some degree, and we feel that the effects of our experiment are similar to what actually occurs in nature.

While it seems that common mussel species are not making substrates more stabile, we think there are still other ways common mussels may be modifying habitats. We already know that mussels facilitate growth of benthic algae (Vaughn et al. 2007), and that other benthic macroinvertebrates respond positively to the increase of this food source (Spooner and Vaughn 2006). Because mussels are thought to feed on algae, and are thought to deposit feed on benthic algae on the sediments (Raikow and Hamilton 2001, Nichols et al. 2005), the common mussel species that dominate mussel beds may be indirectly providing more food for rare mussel species. More study is needed of the possible pathways used by mussels to modify habitats.

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Tables:

Table 1. Summary of substrate parameters and hydraulic parameters modeled at low and high flows.

Parameter (symbol, unit)	**Formula**	**Description**	**Source**
Substrate Parameters			
Mean Particle Size (D, cm)	$\frac{(D_{16}+D_{50}+D_{84})}{3}$	mean particle size of sample	(Folk 1965)
Sorting Index (D S.D., ϕ [converted to cm])	$\frac{(\phi 84-\phi 16)}{2}$	substrate heterogeneity	(Gordon et al. 2004)
Bed roughness (k_s, cm)	$3.5\times D_{84}$	topographical variation of streambed	(Gordon et al. 2004)
Hydraulic Parameters			
Froude number (Fr, dimensionless)	$\sqrt{\frac{U^2}{gd}}$	ratio of inertial to gravitational forces	(Statzner et al. 1988)
Reynolds number (Re, dimensionless)	$\frac{Ud}{\nu}$	ratio of inertial to viscous forces	(Statzner et al. 1988)
Shear stress (τ, dynes/cm^2)	$gsd\rho$	force of friction on substrate	(Statzner et al. 1988)
Shield's entrainment function (τ_*, dimensionless)	$\frac{\rho U_*^2}{gD_{50}\left(\frac{\rho_s}{\rho}-1\right)}$	substrate movement	(Shields 1936)

D_x, substrate particle size (cm) at which x percent of the sample by weight is finer; ϕ, unit of substrate size ($\phi = -\log_2 D(mm)$); ϕx, substrate particle size (ϕ) at which x percent of the sample by weight is finer; d, water depth (cm); U, mean current velocity (cm/s); s, slope of the water line; g, acceleration due to gravity (980 cm/s); ν, kinematic viscosity of water (0.01 cm^2/s); ρ, density of water (0.998 g/cm^3); ρ_s, density of substrate (2.65 g/cm^3) (Shields 1936, Gordon et al. 2004)

Table 2. Summary of mussel data collected on timed surveys by site. Listed for each sites is: time spent searching (minutes), total number of species found, total number of mussels found, and CPUE (catch-per-unit-effort, mussels per minute searched). Also listed are species data: if species was found live (L), and condition of shell if only a shell was found (FD = fresh dead, WD = weathered dead, SF = sub-fossil); a notation of I, II, or III indicates that the species is considered a Tier I, II or III species of greatest conservation need (Spooner et al. 2005, Vaughn 2005).

	Site																
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**11**	**12**	**13**	**14**	**15**	**17**	**18**	**19**
Time Searched (minutes)	60	60	60	60	70	90	120	60	120	60	120	120	120	120	120	120	120
Species found	10	13	11	9	10	11	19	11	19	15	19	18	20	16	17	17	17
Total mussels	104	69	53	60	107	147	392	45	446	120	260	302	575	293	415	342	320
CPUE (mussels/minute)	1.73	1.15	0.88	1.00	1.53	1.63	3.27	0.75	3.72	2.00	2.17	2.52	4.79	2.44	3.46	2.85	2.67
Species																	
Actinonaias ligamentina	L	L	-	L	L	L	L	-	L	L	L	L	L	L	L	L	L
Amblema plicata[III]	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L

Ellipsaria lineolata[I]	-	-	-	-	-	-	-	-	-	L	L	L	L	-	L	-	L
Fusconaia flava	L	-	-	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Lampsilis cardium[II]	L	L	L	L	-	L	L	-	L	L	L	L	L	L	L	L	L
Lasmigona costata	-	-	-	-	-	-	L	-	L	SF	L	-	L	L	L	L	-
Lampsilis fragilis	-	L	-	-	SF	-	-	FD	L	L	-	-	L	L	-	WD	-
Lampsilis siliquoidea	-	-	-	-	SF	-	L	-	WD	-	-	-	-	-	-	L	-
Lampsilis teres	-	L	-	-	L	-	-	-	-	-	L	L	L	L	-	-	-
Megalonaias nervosa[III]	L	-	L	-	-	L	L	L	L	L	-	L	L	L	L	L	L
Obovaria jacksonia[I]	-	-	L	-	WD	-	L	L	L	L	L	L	L	-	L	L	L
Obliquaria reflexa	L	L	L	-	-	-	L	L	L	L	L	L	L	L	L	L	L
Plectomerus dombeyanus	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Pleurobema sintoxia	-	-	-	-	L	L	L	L	L	-	L	L	-	L	L	-	L
Ptychobranchus occidentalis[I]	-	-	L	-	-	-	L	SF	L	-	L	-	-	-	-	WD	L

Potamilus purpuratus[III]	WD	L	-	-	L	-	L	-	-	-	L	L	L	L	-	L	-
Quadrula cylindrica[I]	-	L	L	-	-	L	L	L	L	L	L	L	L	L	L	L	L
Quadrula fragosa[I]	-	-	-	-	-	-	-	-	WD	-	L	L	L	-	L	-	L
Quadrula pustulosa	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Quadrula quadrula	-	L	FD	FD	-	-	L	L	L	L	L	L	L	-	L	L	L
Quadrula verrucosa	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Strophitus undulatus	WD	-	FD	L	-	-	L	-	L	-	-	L	L	-	-	L	-
Truncilla donaciformis	-	-	-	-	WD	-	-	-	L	WD	-	-	-	-	-	-	-
Truncilla truncata	L	L	L	L	L	L	L	-	L	L	L	-	L	L	L	L	L
Utterbackia imbecillus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FD	-

Table 3. Results from quadrat surveys by site. For each site listed are total number of mussel species found, total number of mussels found, and average mussel density (mussels per m^2). Also listed are species data, whether or not a species was found live (X if present); a notation of I, II, or III indicates that the species is considered a Tier I, II or III species of greatest conservation need (Spooner et al. 2005, Vaughn 2005).

	Site					
	9	**10**	**16**	**17**	**18**	**19**
Species found	18	18	17	20	21	16
Total number of mussels	335	137	218	296	327	306
Average mussel density (mussels per m^2)	55.83	22.83	36.33	49.33	54.50	51.00
Species						
Actinonaias ligamentina	X	X	X	X	X	X
Amblema plicata[III]	X	X	X	X	X	X
Ellipsaria lineolata[I]	-	-	X	X	X	X
Fusconaia flava	X	X	X	X	X	X
Lampsilis cardium[II]	X	X	-	X	X	X
Lasmigona costata	-	-	X	-	X	-
Lampsilis fragilis	X	X	X	-	X	-
Lampsilis siliquoidea	-	-	-	X	X	-
Lampsilis teres	X	X	-	X	-	-
Megalonaias nervosa[III]	-	X	X	X	X	X
Obovaria jacksonia[I]	X	X	X	X	X	X

Obliquaria reflexa	X	X	X	X	X	X
Plectomerus dombeyanus	X	X	X	X	X	-
Pleurobema sintoxia	X	X	X	X	X	X
Ptychobranchus occidentalis[I]	-	X	X	-	X	X
Potamilus purpuratus[III]	X	X	-	X	X	-
Quadrula cylindrica[I]	X	-	X	X	X	X
Quadrula fragosa[I]	X	X	-	X	-	X
Quadrula pustulosa	X	X	X	X	X	X
Quadrula quadrula	X	X	-	X	X	-
Quadrula verrucosa	X	X	X	X	X	X
Strophitus undulatus	-	-	-	-	X	-
Truncilla donaciformis	X	-	X	X	-	X
Truncilla truncata	X	X	X	X	X	X

Table 4. Summary of discriminant function analysis on substrate and hydraulic parameters for the presence or absence of mussels in a quadrat. Group means for substrate and hydraulic parameters, discriminant function coefficients, and prediction success are listed for the discriminant function using hydraulic parameters modeled at either low or high flow levels.

Parameter	**Low Flow**			**High Flow**		
	Group Means		*DF*	*Group Means*		*DF*
	Present	Absent	*Coefficient*	Present	Absent	*Coefficient*
D (cm)	0.979	0.409	2.03	0.979	0.409	-0.0991
D S.D. (cm)	0.0256	0.0496	-65.1	0.0256	0.0496	-13.68
Fr	0.102	0.0526	-1.97	0.255	0.246	2.76
Re	2.53×10^{4}	2.21×10^{4}	-2.05×10^{-6}	1.51×10^{7}	1.69×10^{7}	3.37×10^{-7}
τ (dynes/cm^2)	19.9	23.1	-8.33×10^{-3}	115.6	68.9	6.80×10^{-4}
τ_*	3.89×10^{-3}	1.40×10^{-3}	61.9	0.0391	0.213	-22.99
Prediction Success	96%			100%		

Table 5. Summary of discriminant function analysis on substrate and hydraulic parameters for the presence or absence of rare mussel species in a quadrat. Group means for substrate and hydraulic parameters, discriminant function coefficients, and prediction success are listed for the discriminant function using hydraulic parameters modeled at either low or high flow levels.

Parameter	**Low Flow**			**High Flow**		
	Group Means		*DF*	*Group Means*		*DF*
	Common	Rare	*Coefficient*	Common	Rare	*Coefficient*
D (cm)	0.940	1.023	2.20	0.940	1.023	0.170
D S.D. (cm)	0.0256	0.0256	-34.6	0.0256	0.0256	-17.4
Fr	0.0964	0.107	2.15	0.260	0.248	6.74
Re	2.42×10^{4}	2.65×10^{4}	2.04×10^{-5}	1.45×10^{7}	1.57×10^{7}	1.21×10^{-6}
τ (dynes/cm^2)	20.2	19.6	-2.08×10^{-2}	120	111	-1.26×10^{-3}
τ_*	3.75×10^{-3}	4.04×10^{-3}	-13.2	0.0417	0.0361	-53.4
Prediction Success	48%			60%		

Table 6. Summary of quantile regression models ($y = ax + b$) for log-transformed eroded gravel (g) with mussel density as the independent variable.

Quantile	$a \pm$ SE	t	p	$b \pm$ SE	t	p
95	0.008 ± 0.010	0.861	0.390	2.200 ± 0.060	36.538	<0.001
90	0.017 ± 0.006	2.549	0.012	2.100 ± 0.067	31.417	<0.001
75	0.017 ± 0.012	2.545	0.012	1.900 ± 0.058	32.691	<0.001
50	0.000 ± 0.010	0.000	>0.999	1.800 ± 0.079	22.735	<0.001
25	-0.008 ± 0.008	-1.022	0.308	1.600 ± 0.079	20.213	<0.001
10	-0.008 ± 0.010	-0.845	0.399	1.400 ± 0.054	26.045	<0.001
5	-0.025 ± 0.008	-3.113	0.002	1.400 ± 0.000	9.416	<0.001

Table 7. Summary of quantile regression models ($y = ax + b$) for log-transformed eroded gravel (g) with treatment species richness as the independent variable.

Quantile	$a \pm$ SE	t	p	$b \pm$ SE	t	p
95	0.050 ± 0.041	1.223	0.221	2.200 ± 0.087	25.341	<0.001
90	0.050 ± 0.035	1.449	0.149	2.150 ± 0.073	29.330	<0.001
75	0.100 ± 0.031	3.232	0.001	1.900 ± 0.054	35.458	<0.001
50	0.100 ± 0.037	2.695	0.008	1.700 ± 0.064	26.447	<0.001
25	0.050 ± 0.051	0.976	0.330	1.450 ± 0.068	21.310	<0.001
10	0.000 ± 0.081	0.000	>0.999	1.400 ± 0.098	14.278	<0.001
5	0.000 ± 0.066	0.000	>0.999	1.100 ± 0.099	11.129	<0.001

Figures:

Figure 1. Map of mussel sampling sites on the Little River. Sites are labeled in increasing order from upstream to downstream.

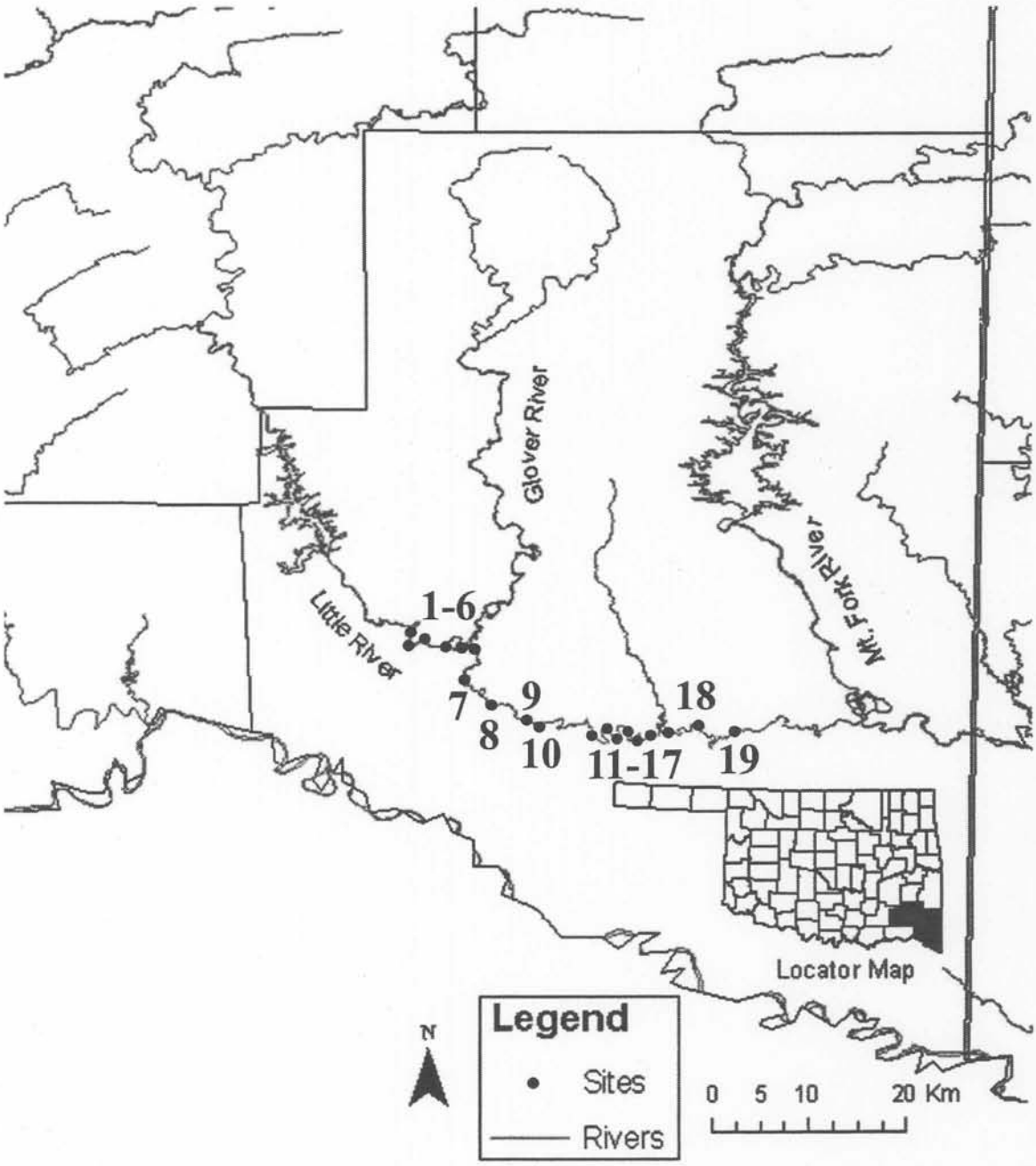


Figure 2. Results of discriminant function analysis using substrate and hydraulic parameters on the presence or absence of mussels in a quadrat. Panels A-B show histograms of the frequency of quadrats with mussels present for a given range of discriminant function scores, while panels C-D show histograms of the frequency of quadrats with mussels absent. Panels A and C show DFA results using hydraulic parameters modeled at low flow levels, panels B and D show DFA results using hydraulic parameters modeled at high flow levels.

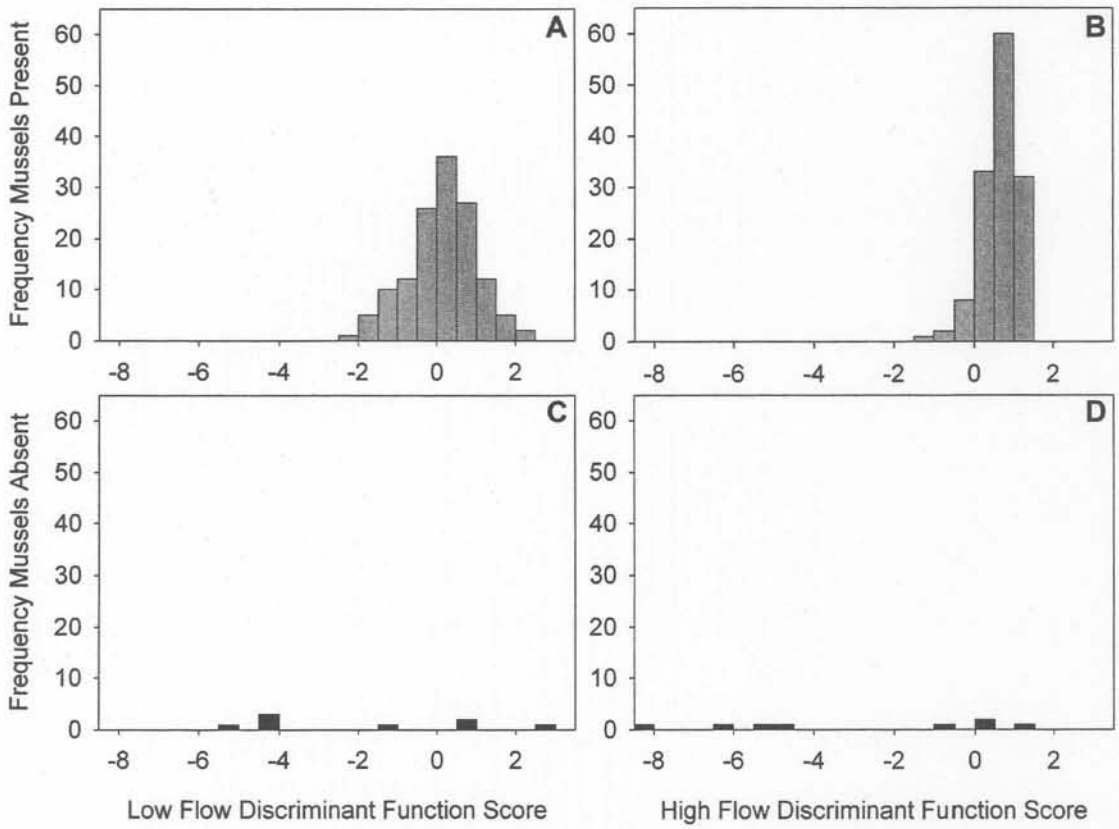


Figure 3. Results of discriminant function analysis using substrate and hydraulic parameters on the presence or absence of rare mussel species in a quadrat. Panels A-B show histograms of the frequency of quadrats with only common mussel species present for a given range of discriminant function scores, while panels C-D show histograms of the frequency of quadrats with rare mussels present. Panels A and C show DFA results using hydraulic parameters modeled at low flow levels, panels B and D show DFA results using hydraulic parameters modeled at high flow levels.

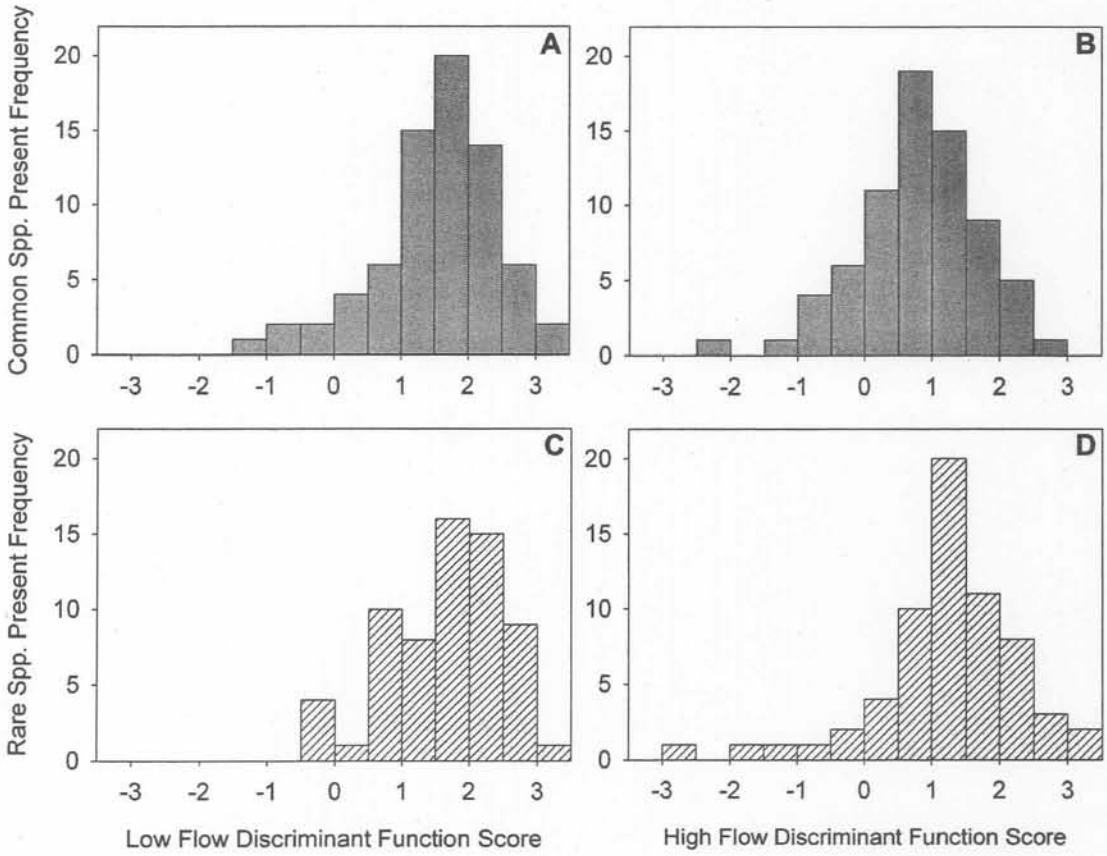


Figure 4. Quantile regressions for log (x + 1) transformed gravel eroded (g) on mussel density. Only significant quantile regression lines are shown (90th, 75th, and 5th), data points are jitter-plotted along both axes to enhance readability.

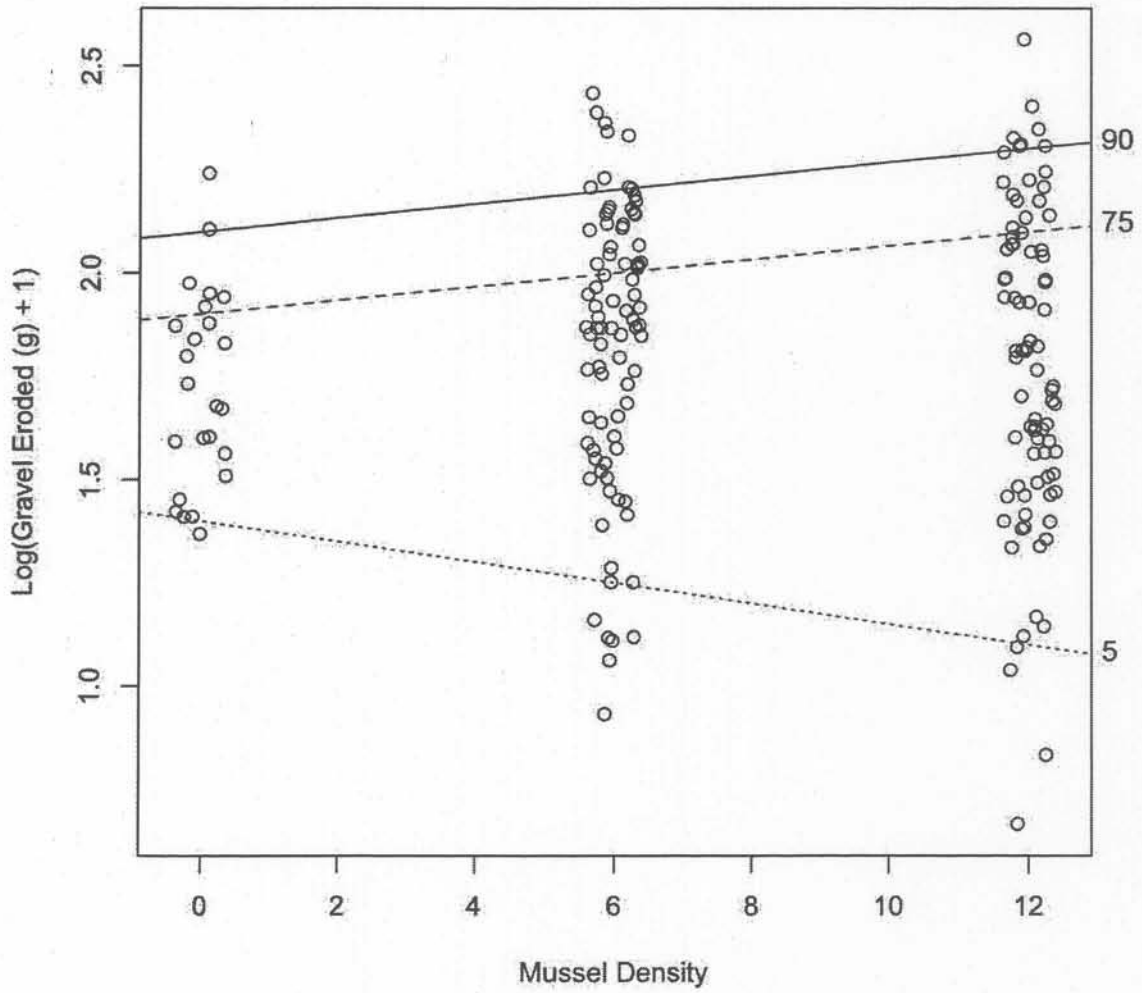


Figure 5. Quantile regressions for log (x + 1) transformed gravel eroded (g) on mussel species richness. Only significant quantile regression lines are shown (75th and 50th), data points are jitter-plotted along both axes to enhance readability.

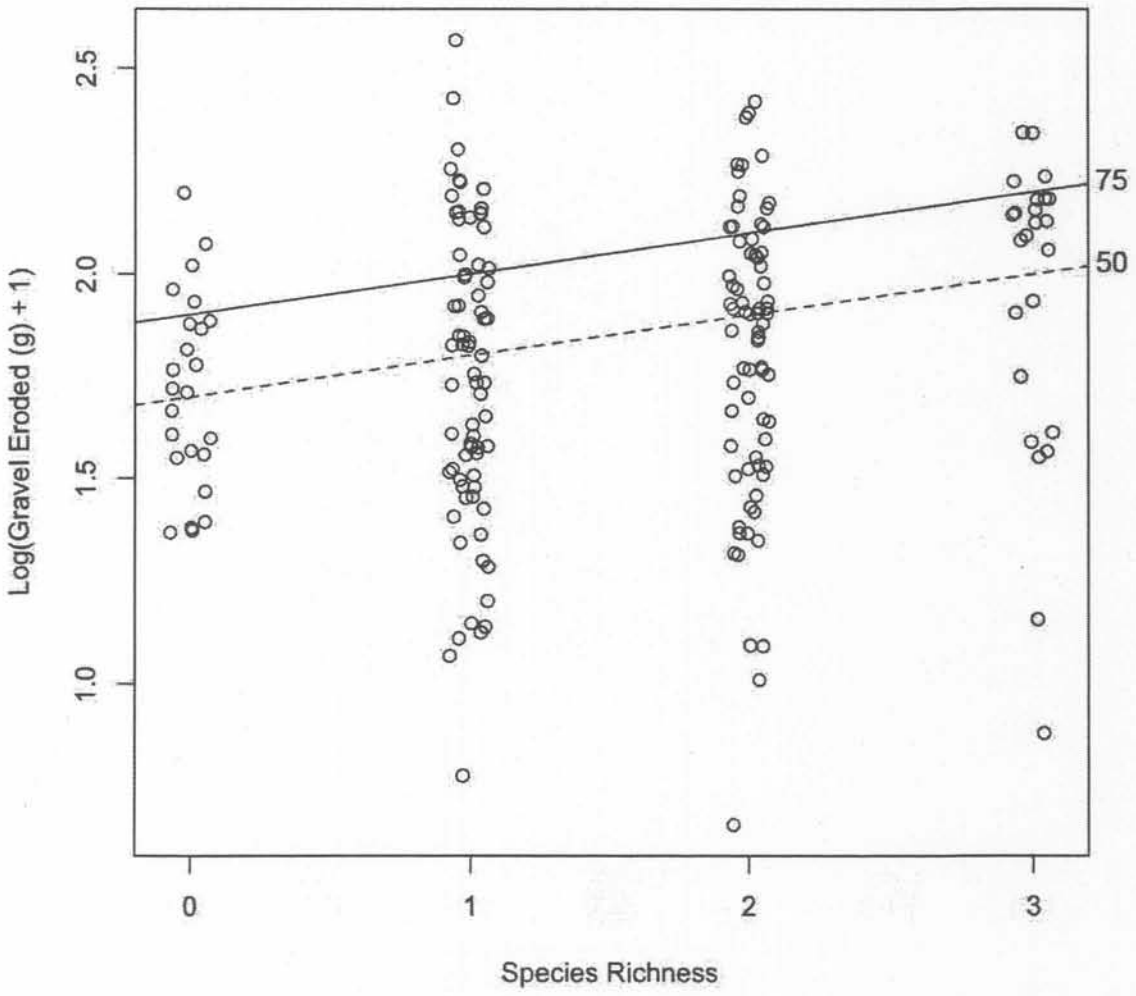
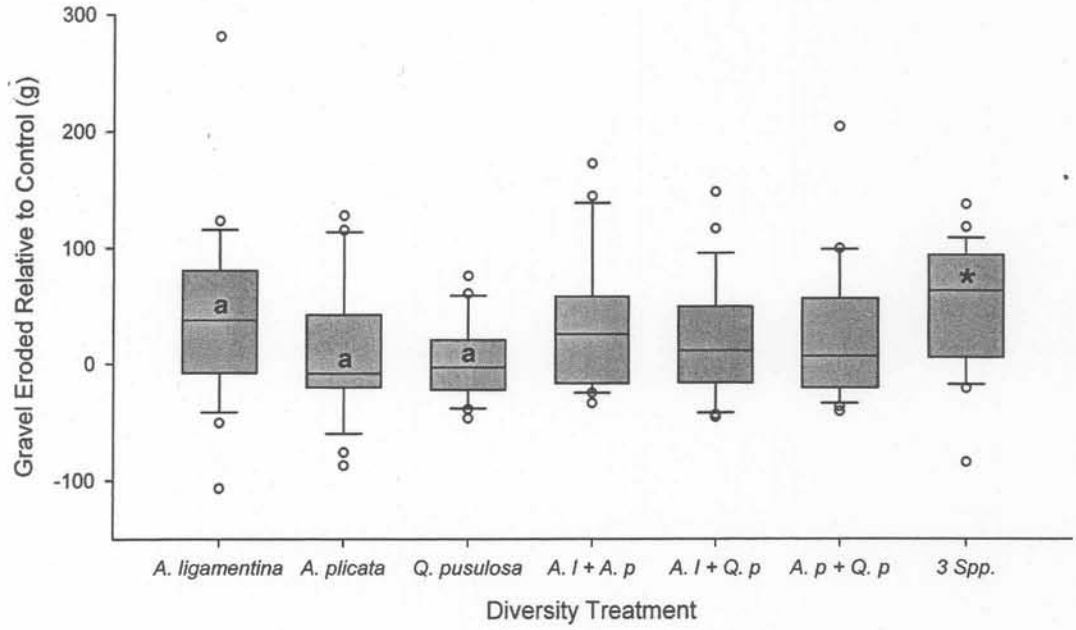


Figure 6. Boxplots showing the effects of diversity treatment on amount of gravel eroded relative to control treatment (g). Boxplots of monocultures that share a letter are not significantly different, and multiple species treatments with an asterisk are significantly different than the expected value based on additive effects of monocultures.



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