FINAL PERFORMANCE REPORT

Federal Aid Grant No. F11AF00027 (T-57-R-1)

Developing a Multiple Spatial Scale Model to Predict the Distribution of Oklahoma's Freshwater Mussel Assemblages with an Emphasis on the Small Rivers of Southeastern Oklahoma

Oklahoma Department of Wildlife Conservation

June 1, 2011 through December 31, 2014

FINAL PERFORMANCE REPORT

State: Oklahoma **Grant Number**: F11AF00027 (T-57-R-1)

Grant Program: State Wildlife Grants

Grant Title: Developing a Multiple Spatial Scale Model to Predict the Distribution of Oklahoma's Freshwater Mussel Assemblages with an Emphasis on the Small Rivers of Southeastern Oklahoma

Grant Period: June 1, 2011 – December 31, 2014

Report Period: June 1, 2011 – December 31, 2014

Project Leader: Shannon Brewer, Oklahoma State University

Objectives:

Phase I
Determine the distribution and presence of mussel beds on several small rivers in southeastern Oklahoma. We will use appropriate materials (e.g., U.S. Geological Survey geologic formation digital maps, digital orthophoto quadrangle, topographic maps, past survey data and peer-review literature) and field reconnaissance (traditional mussel surveys and sidescan sonar) to locate mussel beds on the Middy Boggy and Clear Boggy rivers in southeastern Oklahoma. A subset of these beds will be sampled to determine the relative abundance of individual species. It is anticipated that little emphasis would be placed on the Kiamichi-Little River basin since relatively recent survey data exist for this system (Galbraith et al., 2008). We will attempt to obtain some data already collected from this basin to use in model building and/or validation portions of the study. Habitat and geomorphic data will be collected at several sites where species presence and abundance were determined. We will also use maps and GIS to identify appropriate reach and landscape-level variables for the development of predictive models. The mussel data will be incorporated into a GIS database that could be used to identify significant landscape-level risks to these assemblages (e.g. river access points, highway overpasses, permitted wastewater inputs).

Phase II
Field Data and existing data will be used to generate a model predicting the distribution of mussel beds- and a subset of individual species. The model will be used to identify potential mussel beds on rivers not sampled in Phase I, and validated using standard field techniques.

Summary of Progress:
The objectives were satisfied. See attached final report from Oklahoma State University.

Significant Deviations:
None.

Prepared by: Shannon Brewer and Jarrod Powers
Oklahoma Cooperative Fish and Wildlife Research Unit,
Oklahoma State University Stillwater

Date: February 2015

Approved by:

Fisheries Division Administration
Oklahoma Department of Wildlife Conservation

Andrew K. Crews, Federal Aid Coordinator
Oklahoma Department of Wildlife Conservation

DEVELOPING A MULTIPLE SPATIAL SCALE MODEL TO PREDICT THE DISTRIBUTION OF OKLAHOMA'S FRESHWATER MUSSEL ASSEMBLAGES WITH AN EMPHASIS ON THE SMALL RIVERS OF SOUTHEASTERN OKLAHOMA (SWG T-57-R1)

Final Report, February 2015


Shannon K. Brewer
U.S. Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit
Oklahoma State University
007 Agriculture Hall
Stillwater, Oklahoma 74078
phone: 405-744-9841 | fax: 405-744-5006
e-mail: shannon.brewer@okstate.edu

Jarrod Powers
Oklahoma Cooperative Fish and Wildlife Research Unit
Oklahoma State University
007 Agriculture Hall
Stillwater, Oklahoma 74078
phone: 405-744-9841 | fax: 405-744-5006
e-mail: jarrod.powers@okstate.edu

EXECUTIVE SUMMARY

Freshwater mussels represent an imperiled taxa worldwide. The National Strategy for the Conservation of Native Freshwater Mussels (1998) identified ten concerns related to the conservation of freshwater mussels including: 1) increasing knowledge of habitat suitability, 2) identifying specific mussel relocation and introduction sites, and 3) evaluating distributions and population dynamics of species. The objectives of this project were 1) determine the distribution and presence of mussel beds in the Muddy and Clear Boggy rivers, and 2) determine environmental factors at multiple spatial scales related to the distribution of a subset of individual mussel species found in the Muddy and Clear Boggy rivers. Because the Muddy and Clear Boggy rivers are deep and turbid lotic systems, the first step was to assess a method (sidescan sonar) to assist in identifying the location of mussel beds in hazardous (e.g., deep, turbid, and with a large influx of woody debris) portions of the rivers. The validation confirmed that ~60% of the sites had mussel beds and ~80% had some mussels or shells present. Water depth was significantly related to our ability to predict mussel-bed locations: predictive ability was greatest at depths of 1–2 m, but decreased in water > 2-m deep suggesting use of a tow fish would improve the likelihood of detection. We determined that sidescan sonar was an effective tool for preliminary assessments of mussel presence during times when they are located at or above the substrate surface and in relatively fine substrates excluding fine silt. Sidescan sonar data were then combined with traditional survey data to build models predicting mussel-bed locations, species presence, and species densities. Generally, we found our predictions of mussel-bed locations and species presence to be inadequate, probably due to the dispersed nature of beds in both rivers. The only exception was the model predicting Wabash pigtoe *Fusconaia*

flava presence (pseudo $R^2 = 0.36$). Densities of mussel species with few host fishes showed significant relationships with increasing densities of their respective host fishes (bleufer *Potamilus purpuratus*, $R^2 = 0.41$; fragile papershell *Leptodea fragilis* $R^2 = 0.46$). Models predicting freshwater mussel densities performed much better than presence models with drainage area, width:depth ratios, and % of shale geology selected most often as influential variables. Models predicting Wabash pigtoe densities suggested, unlike most species, this species was quite tolerant of modified land use as densities were exceptionally high in areas with relatively high percent agriculture and pasture land use (66%-73%). Finally, we assessed the movements of different mussel species to provide some insight into how some of these species are able to make movements in response to some forms of environmental perturbation. Several mussel species (bleufer, Wabash pigtoe, threeridge- *Amblema plicata*, fragile papershell, and yellow sandshell- *Lampsilis teres*) were tagged in summer and autumn 2012. External tagging via PIT tags occurred at four sites and was initiated during the baseflow period (August-September 2012). Movement did not differ by species but did with time, with individuals moving the most during the early portion of the reproductive period (March, ~ 4 meters). Only fragile papershell showed a positive relationship between movement and discharge (Adj R^2=0.27, P=0.06) but this relationship was only found at one site (CB5). This relationship is likely the result of low sample size and the significant influence of one data point suggesting it should be interpreted with caution. The results of our study provide information on what environmental factors are most likely to influence species densities, which can guide conservation initiatives. This research can help managers decide what areas or species may be most suitable for reintroductions and where and what improvements can be made to the landscape to benefit mussel conservation.

Background

Freshwater mussels continue to decline despite recognition of the valuable role they play in aquatic ecosystems. Mussels provide important ecosystem functions by filter feeding (i.e., releasing nutrients into the substrate; Vaughn et al. 2004, Vaughn et al. 2008), oxygenating sediment with burrowing behavior (Vaughn and Hakenkamp 2001, Howard and Cuffey 2006), and providing valuable food to other organisms (Tyrrell and Hornbach 1998, Tiemann et al. 2011b, Bódis et al. 2014).

Globally, freshwater mussels are one of the most threatened and endangered groups of organisms (Watters 1994a, Strayer and Dudgeon 2010). Of the nearly 300 species found in the U.S., 70% are of conservation concern (Williams et al. 1993, Master et al. 2000). The National Strategy for the Conservation of Native Freshwater Mussels (National Native Conservation Committee 1998) identified ten concerns related to the conservation of freshwater mussels and although some progress has been made in several areas (e.g, increased knowledge of mussel biology, improved mussel-propagation programs, increased funding for mussel conservation), conservation concerns still focus on several areas including: 1) increasing knowledge of habitat suitability, 2) identifying specific mussel relocation and introduction sites, and 3) evaluating distributions and population dynamics of species (Haag and Williams 2014).

Declines in freshwater mussel populations relate to several abiotic and biotic factors associated with landscape change: habitat destruction, water-quality degradation, hydrologic change, and declines of host fish (Downing et al. 2010). Habitat degradation is a leading cause of mussel declines (Downing et al. 2010), particularly in riparian areas (Newton et al. 2008).

Changes from high-quality to low-quality habitat are linked to losses in freshwater mussel diversity and abundance (Osterling et al. 2010). Changes in land-use practices alter the quantity, timing, and duration of sediment and discharge to the stream, which negatively affect the composition and distribution of mussels (Box and Mossa 1999). Further, dam construction and increased water use alter the natural flow regime, preventing fish-host passage (Watters 1996), reducing host abundance (Bogan 1993), and reducing the availability of suitable substrates for mussels (Layzer and Madison 1999). To further exacerbate the situation, climate change is expected to alter precipitation and temperature patterns (Girvetz et al. 2009) that could alter the richness and distribution of mussels via several mechanisms: decreased reproductive fitness (Spooner and Vaughn 2008), desiccation or species displacement via flow alterations (Galbraith et al. 2010), and decreased growth via nutrient availability (Smith et al. 2006). Though we have increased our understanding of how some human-induced threats on the landscape affect mussel distribution and abundance (Box and Mossa 1999, Downing et al. 2010), there is limited information on how these factors interact across spatial scales to determine mussel distributions and abundances.

Efforts to understand the influence of habitat on mussel distribution and abundance progressed from fine (e.g., microhabitat) to coarse (e.g., landscape factors) spatial scales over time with substantial discrepancy in the relative importance of each scale. Initial investigations were based on microhabitat features (e.g., water depth, Strayer 1981; velocity, Layzer and Madison 1999), but investigators showed discrepancy in the importance of these features (Strayer and Ralley 1993, Brown et al. 2010). Macrohabitat variables were found to be significant in some studies aimed at juvenile distributions (e.g., shear stress, Strayer 1999, Layzer and Madison 1999, Morales et al. 2006; current velocity, Layzer and Madison 1999), but

these were often not good predictors of adult mussel distributions (DiMaio and Corkum 1995, Layzer and Madison 1999, Hardison and Layzer 2001, Allen and Vaughn 2010). At the reach (often 40 times wetted width) or stream segment (tributary to tributary confluence) scales, studies found hydraulic factors (Steuer et al. 2008), sinuosity (McRae et al. 2004), and habitat degradation (Box and Mossa 1999) correlated with mussel abundance. More recent studies have indicated landscape variables are significant predictors of mussel distribution and abundance (e.g., rabbitsfoot *Quadrula cylindrica*, Hopkins 2009; freshwater pearl mussel *Margaritifera margaritifera*, Wilson et al. 2011; and eastern elliptio *Elliptio complanata*, Cyr et al. 2012). Landscape variables significantly related to mussel distributions include structuring variables (e.g., stream size, Atkinson et al. 2012; watershed geology, McRae et al. 2004, Atkinson et al. 2012, Daniel and Brown 2013), more ecologically-based variables (e.g., landscape fragmentation, Shea et al. 2013), and other factors related to landscape changes (e.g., agriculture and urban land use, Shea et al. 2013; urban development, Brown et al. 2010; sedimentation, Williams et al. 1993; riparian land use, McRae et al. 2004). Despite recognition of the influence of landscape factors on aquatic biota, few freshwater mussel studies include factors at multiple spatial scales (Hopkins 2009; but see Daniel and Brown 2013). Effective conservation and restoration strategies would benefit from an examination of factors at multiple spatial scales.

Understanding the importance of variables at different scales relates to the interactions that occur between spatial scales to define suitable habitat and the investigator's abilities to identify such habitats. Interactions operate between ultimate, intermediate, and proximate factors (Stevenson 1997) and these relationships may dictate the perceived importance of spatial scale. For example, increased runoff in regions of highly impermeable soils (ultimate factor) is thought to increase runoff to streams and therefore instream sediment (proximate factor) thereby

reducing the abundance of smallmouth bass (Brewer et al. 2007). Depending on the scale of investigation, the perceived relative importance of any variable may change. At a fine scale a factor (e.g., substrate) may be assumed to be important to mussel presence, however, when viewed at a coarse scale we may learn that the association to the substrate was determined by an ultimate factor. Understanding the linkages across scales is essential to understanding what effects they create. Sediment is often implicated as a significant factor leading to contracting distributions and reduced abundances of freshwater mussels (Layzer and Madison 1999) and it is assumed to be related to land-use change (Box and Mossa 1999), but rarely are the two factors across scales included in a single study. Combining factors at multiple spatial scales allows an examination of constraining variables (e.g., stream size) while identifying interactions between ultimate and proximate variables that relate to mussel declines. For example, a species may occupy larger streams but be absent from some reaches due to interactions between soils and land use that lead to excess sedimentation. Understanding cross-scale linkages will enhance the ability of managers to identify areas likely to be successful restoration sites.

The development of conservation initiatives to restore declining freshwater mussel populations requires an understanding of habitat needs and environmental factors that are related to species persistence. Current restoration efforts focus on captive breeding (Thomas et al. 2010) and reintroduction of imperiled species into what is perceived to be suitable habitat (Cope and Waller 1995, Peck et al. 2007). Selection of suitable relocation sites is often based on qualitative criteria (Cope and Waller 1995, Peck et al. 2007). Attempts to reintroduce species without remedying the factors related to the decline or understanding the factors related to success leads to reintroduction failures (Morell 2008). In fact, less than 50% of evaluated mussel reintroductions have been considered successful (Cope and Waller 1995, Peck et al. 2007). For

restoration efforts to be successful, an understanding of how factors at multiple spatial scales interact to alter distribution and densities of freshwater mussels would be beneficial. This information would allow reintroductions to proceed in an informed capacity where appropriate species are chosen based on their ability to tolerate certain forms of environmental perturbation.

Objectives:

The project had two objectives:

1. Determine the distribution and presence of mussel beds on several small rivers in southeastern Oklahoma, with an emphasis on the Muddy and Clear Boggy rivers.
2. Determine environmental factors at multiple spatial scales related to the distribution of a subset of individual mussel species found in the Muddy and Clear Boggy rivers.

Because the Muddy and Clear Boggy rivers are deep and turbid lotic systems, the first step was to assess a method (sidescan sonar) to assist in identifying the location of mussel beds in hazardous (e.g., deep, turbid, and with a large influx of woody debris) portions of the rivers. These data were then combined with traditional survey data to build models predicting mussel-bed locations, species presence, and species densities. Finally, we assessed the movements of different mussel species to provide some insight into how some of these species are able to make movements in response to some forms of environmental perturbation.

Study Area

Sidescan sonar

Sidescan sonar images were captured over a 32-km reach of the Muddy Boggy River and portions of Lake McMurtry (Figure 1). The Muddy Boggy River is a major tributary of the Red

River. The catchment drains 6,291 km^2 including rugged terrain in the headwaters that transition to gentle hills with a wide valley in the lower catchment (Pigg 1977). The Muddy Boggy River meanders through three major ecoregions but the study reach was located in the South Central Plains ecoregion where dominant soils are calcareous sands, clays, and gravels. The Muddy Boggy River has a dendritic drainage pattern and a gradient that ranges 7.9-26.4 m/km (Pigg 1977). The study reach was selected because it supports existing freshwater mussel beds and includes several deep (> 2 m) pools. The lower portion of the river is characterized by long, deep pools separated by run and riffle complexes. Dominant substrate varies from coarse (e.g., cobble) to fine (e.g., clay) materials. This reach of the Muddy Boggy River was ideally suited for this study because the physicochemical characteristics present make traditional freshwater mussel sampling protocols difficult to perform. The river carries high suspended sediment loads even during base-flow conditions and has an abundance of instream woody debris. Lake McMurtry is a 1,155-acre eutrophic reservoir located in Noble County, Oklahoma. Lake McMurtry was impounded for flood control, water supply, and is used for recreation. Average turbidity of the reservoir is 20 NTU (OWRB, http://www.owrb.ok.gov/quality/monitoring/bump/pdf_bump/Current/Lakes/McMurtry.pdf, Accessed March 31, 2014).

Mussel distributions

The location of the Muddy and Clear Boggy rivers is a unique study system for examining landscape-level effects because the rivers are highly diverse and traverse several physiographic regions, thus creating a variety of different physiochemical conditions to which mussels may

respond. The Muddy Boggy basin drains 6,291 km^2 beginning with rugged terrain in the headwaters and transitioning to gentle hills with a wide valley in the lower portions of the basin (Pigg 1977). The basin drains portions of the following physiographic regions: Arkansas Valley, Ouachita Mountains, South Central Plains, and includes portions of the Cross Timbers. The Arkansas Valley is underlain by shale, sandstone, and coal with a mixture of oak woodland, tall grass prairie, oak–hickory forest, and oak–hickory–pine forest. Streams in this region tend to have deep pools. The Ouachita Mountains ecoregion is underlain with sandstone and shale with oak–hickory–pine forest. Streams in this region are moderately clear to highly turbid. The South Central Plains is underlain by calcareous sands, clays, and gravels with mostly oak–hickory–pine forest. Streams in this region typically have good water quality and share similarities with the Ouachita Mountains. The lithology of the Cross Timbers is limestone, dolomite, and sandstone with oak savanna, scrubby oak forest, eastern redcedar, and tallgrass prairie in the region. Streams are typically shallow and with sandy substrates (Woods et al. 2005). Both the Muddy Boggy and Clear Boggy rivers have dendritic drainage patterns and gradients that range from 7.9 - 26.4 m/km (Pigg 1977). Rainfall within the basin ranges from 109 – 145 cm annually.

Methods

Sidescan sonar to detect mussel beds in deep-water habitats

We used a sidescan sonar system (Humminbird® 1198c SI system, Eufaula) to capture images of the river-bed topography during base-flow conditions in July 2012 and elevated discharge in May 2013. The surveys coincided with a portion of the freshwater mussel reproductive and feeding period (April through July) when mussels were more likely to be at the substrate surface

(Galbraith and Vaughn 2009). Sidescan surveys were completed in 1-2 d so discharge conditions would be relatively constant on each scanning day.

The sidescan sonar unit was set up to reduce image distortion and capture as much detail as possible in the images. Sidescan surveys were conducted with the sidescan unit mounted on the front of a canoe with the transducer to prevent the wake from causing image distortion. We mounted a 3.5 hp outboard motor on the back of the canoe to allow for speed control of approximately 6.5 kph. Consistent speed control was important to ensure the sidescan capture completely covered the stream bottom and to prevent major distortion in imagery detail. Multiple scanning frequencies were tested: low frequency (down-facing beam- 83 kHz, and sidescan beam- 455 kHz), high frequency (down-facing beam- 200 kHz, and sidescan beam- 800 kHz), and a combination of the two frequencies (down-facing beam- 83 kHz with sidescan beam- 800 kHz and down-facing beam- 200 kHz with sidescan beam- 455 kHz). Higher frequencies for both the sidescan beam and the down-facing beam were selected because they resulted in the most detailed images. All sidescan images were captured from approximately a mid-channel position. Sidescan surveys captured images directly below the canoe, and to both sides of the canoe. Captured sidescan images were recorded as video files and the corresponding GPS coordinates were recorded to a secure digital high capacity (SDHC) memory card in the sidescan head unit.

Sidescan images were imported into specialized software (Dr. Depth®, Göteborg, Sweden) to be processed and mended. Processing the images was required as the raw images were not compatible with geographic information system (GIS). Images were processed into a complete mosaic using Dr. Depth. Original sidescan images have two parts: one for images captured to the right of the canoe and one for images captured to the left. Both of these image parts have to be

selected to allow the image to be centered within the mosaic. Mosaic settings for the internal map size were changed to 500 m by 500 m to provide the most detail in the selected images. The pixel size of the image was set within Dr. Depth to match the original pixel size (3.125 cm) to maintain adequate resolution. After the image was centered within the mosaic tool, it was converted to a map image and saved as a KML (.kml) file.

Map images were imported into GIS software, ArcMap 10 (Environmental Systems Research Institute, Redlands). The new file images were georeferenced to aerial photographs by gathering the geographic extent information from the file properties. A notepad document was created using the extent data and GPS coordinates from the KML file. This information was linked to the image file and rectified in ArcMap. The cell size was changed to 0.0000003 and the resample type was changed to bilinear interpolation (for continuous data). The file format was then changed to a grid file for use in ArcMap for map-image evaluation.

We developed a series of reference images for identifying potential mussel beds from our river images. Our first set of images was developed by scanning at a nearby reservoir (Lake McMurtry, Stillwater, Oklahoma, USA, Figure 1). We located several areas of dominant substrate material: 1) sand (< 2 mm), 2) gravel (2-50 mm), and 3) cobble (50–250 mm). We delineated a 9-m^2 area of relatively homogenous substrate material and scanned the areas multiple times to capture several images without any mussel shells present. Multiple scanning passes were made directly over the survey area and at varying distances (5 m and 15 m) from the outside edge of the survey area. Next, we placed 50 mussel shells (multiple species) of different sizes throughout the selected 9-m^2 area. All shells were buried 2/3 to 3/4 into the substrate leaving the posterior portion of the shell protruding to reflect how a mussel would be positioned naturally. Several sidescan sonar passes were then completed with the mussel shells in place. We

examined the characteristics of the reflected properties at known mussel-bed locations looking for commonalities in the images. We then used the reference key to examine the sidescan images taken from the river for areas with similar clustering reflectance.

We compared our reference images to river-survey images to determine where mussel beds might be present on the Muddy Boggy River. We identified 94 areas within the images to be potential mussel beds. Each of these locations was assigned to one of three categories based on the potential of containing a mussel bed: high, intermediate, and low. We haphazardly chose a subset of these potential sites (n = 17) for field validation. Field validation used two approaches: divers using self contained underwater breathing apparatus (SCUBA) and tactile snorkeling. SCUBA was used to assess mussel presence in deep (> 1 m) portions of the study site. Three to four individuals were approximately evenly spaced across the deep portion of the river channel. Divers searched the river bed using tactile searches as visibility was extremely limited (< 10 cm). In addition, tactile searches via snorkeling were performed in shallow-water sections (≤ 1 m, often the inside bend of the river) by three or four additional individuals to ensure adequate coverage of each site. We recorded the presence of any mussel shells in addition to approximate densities within the area examined. We defined a mussel bed as an area with a minimum of one mussel every 2 m (a minimum of 1 mussel per m^2).

Habitat characteristics were measured at each of the 17 sites where field validation occurred. We haphazardly measured depth (1.0 cm) at 3-6 points at each site. Number of points measured depended on the size of the area sampled and the extent of the mussel bed. Dominant substrate type was determined at each site via tactile searches using a modified Wentworth scale (gravel 2-15 mm, pebble 16– 63 mm, cobble 64–256 mm, boulder >.256 mm, and bedrock; Bovee and Cochnauer 1977). We measured average water-column velocity at 0.6 from the water's surface

(if < 0.8 m) or averaged measurements from 0.2 and 0.8 from the surface (when ≥ 0.8 m) using an electromagnetic flow meter (Marsh McBirney, Loveland). Mean depth and velocity and the coefficient of variation were calculated from subsamples taken at each site. Bankfull width (0.10 m) and depth (0.10 m) were measured one time at each site following methods of Gordon (2004).

We developed a logistic regression model to examine the relationship between mussel bed presence and several habitat variables. Analyses were conducted using Statistical Analysis Systems (SAS Institute, Carey). Explanatory variables were evaluated for multicollinearity using Spearman's rank correlation coefficient procedure to exclude variables that were highly correlated from the final model. Statistical significance of Spearman's rank correlation coefficient procedure was not used as it does not necessarily identify highly correlated variables. Instead, a cutoff of $r \geq 0.30$ was used to define variables as being multicollinear (Graham 2003). To prevent the bias associated with including multicollinear variables in multiple regression analyses, we selected a subset of correlated variables for model building that we hypothesized would have the most influence on mussel-bed locations. Additionally, we excluded variables that had little variation across study sites. The final set of variables were used to create a logistic regression model using forced entry (forced logistic regression; Colombet et al. 2001). If the model was significant, standardized coefficients were calculated to determine the importance of the explanatory variables in the model. An interaction term (depth*sinuosity) was fit to an additional model to evaluate whether the contribution was significant to the model. We completed diagnostic procedures using residual plots (Pearson and Deviance) to identify observations that were not explained well by the model. We also examined influence statistics (DFBETA, DIFDEV, and DIFCHISQ) to measure changes in the coefficients if an observation was deleted (Allison 1999).

Identifying freshwater mussel presences

Freshwater mussel presence and densities were determined using a two-stage sampling approach. The first stage was completed in summer 2011 to identify broad-scale longitudinal distributions on the Muddy and Clear Boggy rivers (Figure 2). Each river was divided into 10, 32-km segments and six segments on each river were haphazardly selected (based on access). We attempted to sample three riffles, runs, and pools at each site, but sometimes it was not possible because depths were > 1 m. Strip transects (Strayer and Smith 2003) were established perpendicular to the direction of flow at 10-m intervals in large channel units (≥ 40 m) and at five evenly-spaced intervals in smaller channel units (< 40 m). A weighted line was placed across each transect and two people swam each transect, performing tactile searches approximately 1-m upstream and downstream of the lead line. When mussels were encountered, we estimated approximate densities across the area sampled to assess whether the area was considered a bed (a minimum of 1 mussel per m^2). The spatial extent of the bed ended when no mussels occurred within 2 m of another mussel. Estimated mussel densities and the associated spatial extent were used to categorize each mussel bed: a large mussel bed (mussel density > 10 per 1 m^2 and covering > 500 m^2), intermediate mussel bed (mussel density > 10 per 1 m^2 and covering < 500 m^2), and small mussel bed (0 - 5 mussels per m^2) (Christian and Harris 2005b) but these data were only used to develop models predicting mussel presence. Freshwater mussels were identified on site using common shell characteristics, measured (shell length and height, 1.0 mm), and then redistributed on the transect where they were collected.

The second stage of sampling focused on determining densities of individual species, identifying rare species and juveniles. Systematic sampling occurred at six sites (MB1, MB8,

MB11, CB1, CB3, and CB10) in summer 2012 and four sites (MB2, MB10, CB2, and CB9) in summer 2013 (Figure 2). Previous sampling was conducted at the sites to confirm the spatial extent of the mussel beds. We created a grid over each bed that comprised 1-m^2 quadrats and covered a mussel bed up to 200 m^2 (beds > 200-m^2 in length required additional sampling). We then sampled 10-20% of the mussel bed depending on the depth of the water (i.e., some areas were too deep to sample safely, > 1 m) and the random start location (i.e., quadrats were sampled ≥ 1 m apart to approximate independence). If a quadrat was selected but was unsafe to sample, then an additional random quadrat was selected. Each selected quadrat was first sampled using a tactile approach on the surface of the substrate (Metcalfe-Smith et al. 2000). Tactile searches involved feeling the substrate by hand from the surface to a depth of ~5 cm. Next, we excavated the substrate within each quadrat to a depth of 15 cm and placed contents into a 0.25 m^2 sieve to find any burrowed mussels (Vaughn et al. 1995). The sieve mesh was 6 mm because that mesh size is most effective for detecting juveniles (Smith et al. 2001). Freshwater mussels were identified on site, measured (shell length, height, and width, 1.0 mm), weighed (0.01 g) and then redistributed in the sampled quadrat. Mussel densities were expressed per 10 m^2 at each sampling site.

Fish sampling near known mussel beds

Six fish-sampling sites were longitudinally stratified on the two rivers: three on the Clear Boggy River and three on the Muddy Boggy River (Figure 2). Selected sites were in close proximity to known mussel-bed locations that were identified during mussel sampling in summer 2011. Two of the sites on each river had a high occurrence of mussels whereas one site on each river had a

low occurrence of mussels. We sampled a series of channel units at each site that included a run, riffle, and pool.

Fish sampling was conducted over two years and two seasons to coincide with the two distinct mussel-brooding periods: tachytictic (breeding occurs in the spring and glochidia are released during the summer) and bradytictic (breeding occurs in the summer and glochidia are released the following spring). Sampling was completed in late June 2012 and included all six sampling sites. The second phase of sampling was completed in mid to late March 2013 and included five of the six sampling sites. One site (MB3) was not resampled because of difficulty accessing private lands. Gill nets, hoop nets, electrofishing, and seining were all used to sample the fish community to account for differences in habitat use by fishes and gear bias via different fish species (Bonar et al. 2009). Gill nets (~23-m in length with three equal length monofilament mesh panels with bar mesh sizes of 25.4-mm, 50.8-mm, and 76.2-mm) were soaked 6-8 h in deep-water habitats. A series of hoop nets (small 2.4 m long, 25 mm bar mesh, with seven 0.61 m hoops; medium 3.4 m long, 25 mm bar mesh, with seven 0.76 m hoops; large 3.7 m long, 50.1 mm bar mesh, with seven 0.91 m hoops; Miller Net and Twine Co., Inc, Memphis, TN) were set in run habitats (one series upstream and downstream) parallel to the river bank and remained set overnight (~24-hrs). Hoops were orientated downstream while the cod end was positioned upstream and each hoop net was baited with 1 kg of ground cheese logs (Boatcycle, Inc., Henderson, Texas). Each hoop net had the throat constricted following recommendations by Sullivan and Gale (1999). The same run was then sampled for 30-60 min using a seine (2.9 m wide by 1.9 m high, 4 mm mesh) and techniques described by Bonar et al. (2009). We combined seining and backpack electrofishing (60 Hz, pulsed DC with a 10-15% duty cycle with voltage settings around 220-280, Bonar et al. 2009) to sample fishes (30-60 min) from shallow-water

portions of each reach. All fishes were identified to species and released downstream of our sample area or preserved in 10% formalin and later identified in the laboratory.

Fishes collected were inspected for infection by freshwater mussel glochidia on their gills and fins. Any fish that could not be identified in the field was preserved in 10% buffered formalin and brought back to the lab for later identification. Fish suspected of being infected with mussel glochidia were euthanized with an overdose of MS-222 (250mg/l). The operculum was removed to allow for inspection of the gills. Potentially infected gills were clipped and preserved in a tissue vial with 99% ethyl alcohol. The same preservation process was used for potentially infected fins. Collected fish gills and fins were analyzed using a dissecting scope. Areas of apparent infection on the gills that could not be identified under the dissecting scope were placed on glass slide and viewed under a microscope. Gill tissue was then rinsed and preserved in 99% ethyl alcohol.

We developed simple linear regressions to examine the relation between fish-host abundance (independent variable) and mussel species density (dependent variable). Fish-host data were expanded to include additional sampling sites that were in the same river segment. For example, if fish-hosts were sampled at one site and other sampling sites occurred in the same river segment (tributary to tributary), we assumed that the same fish would occur at other sampling sites in close proximity (within the same river segment). Model assumptions for normality were evaluated using the Anderson-Darling test and normal quantile plots. Variables were natural log transformed to satisfy the assumption of normality. We added one to all data before log transformation to deal with zeros within the data set. Statistical analyses were performed using Statistical Analysis Systems (SAS Institute, Carey, NC, USA).

Environmental features at multiple spatial scales

Habitat data (Table 1) were collected at multiple spatial scales (Table 2): catchment, segmentshed, reach, channel unit, and microhabitat. Landscape factors were calculated as the proportion of each variable included in the catchment draining to each study site (e.g., proportion of geology). Segmentshed variables were calculated over the catchment portion draining from one tributary confluence to the next. Segmentshed data were then trace accumulated upstream from each sample site to include the proportion of the landscape variable that would influence each sample site. For example, we calculated the proportion of each geology type from each sample point upstream to represent the influence geology had on the water quality of each site (i.e., downstream geology would be insignificant). A reach was classified as 40 times the channel width. Channel units (CU) were classified using descriptions provided by Peterson and Rabeni (2001) and collapsed into three simple habitats: riffle, run, and pool. Fast, shallow flows over medium to large substrate with higher gradients were classified as riffles. Smooth, unbroken flow that often transitioned riffles and pools and had moderate velocities were classified as runs. Areas with slow flowing and often deeper water (but some may also be shallow), typically on the outside of a bend, were classified as pools. Microhabitats were homogenous patches within CU (e.g., depth, and substrate composition).

Existing geospatial data were used to obtain information on catchment and segmentshed habitat variables for each site (Table 3). We calculated the drainage area for the upstream area of the catchment draining to each site (1 km^2; Drain) using ArcMap. The proportion of lithology was measured for each segmentshed using the National Scale Geology layer and ArcMap (NRCS). Using the Soil Survey Spatial and Tabular data layer, we were able to classify soil types into one of three categories of soil erodibility: highly erodible land, potentially highly erodible land, and not highly erodible (Benbrook 1988). We then measured the proportion of highly

erodible land (HEL) for each segmentshed. Sinuosity (Sin) was calculated for each segmentshed using ArcMap by measuring the distance along the channel and then dividing by the direct line-of-site between the two ends of the reach (Kaufmann et al. 1999).

We created a buffer area around each study site to identify the influence of habitat factors at more fine scales. The buffer started at the farthest downstream point of the study reach, extended 1 km in the upstream direction and covered 100 m on each side of the bank (~200-m total). We used aerial photographs of the catchment (NAIP; Table 3) and clipped this to our selected buffers. We then delineated the clipped buffer area by creating polygons around agriculture and pasture land (Land), forested vegetation (Forest), and riparian corridor width (Rip) and then we calculated proportions within the buffer for each variable.

Several reach-scale factors were measured at each sampling site. Bank-soil composition (Bank) was measured to quantify bank stability and erosion potential using Munsell's Soil Chart to measure soil color and texture at each site and cross referenced with USGS soil layers (Table 3). Bankfull width and depth were measured using methods described by Gordon (2004) as an index of cross-sectional shape and later used to calculate width-to-depth ratios (WD).

Microhabitat factors were measured at all sampling sites. Substrate composition was visually estimated using a modified Wentworth scale (previously described). In areas where only gravel-sized particles or finer occurred (silt 0.059 mm, sand 0.06–1.00 mm, gravel 2mm; Bain 1999), a shovel of substrate was removed, dried, sieved (2 mm and 150 microns), and weighed to determine percentages of each fine substrate group.

Hypotheses and models predicting mussel bed, species presence, and species densities

We developed *a priori* hypotheses to predict the habitat factors at multiple spatial scales that had the greatest influence on species presence (Table 4) and density (Table 5). Hypotheses were developed based on existing literature. Four hypotheses were developed for species presence and species density using habitat factors that are thought to have the greatest influence on each species: drainage area, land use, riparian vegetation, forest cover, soil, sinuosity, width-to-depth ratios, and substrate. Fish-host data were not incorporated into the hypotheses because these data were only collected at a subset of sites to better understand the longitudinal changes. Drainage area is a key factor influencing the longitudinal continuum of aquatic habitat (Strayer 1993, Dodds et al. 2004, Atkinson et al. 2012). Bleufer *Potamilus purpuratus* and fragile papershell *Leptodea fragilis* have specific longitudinal preferences and are most abundant in the downstream portions of large rivers (Cummings and Mayer 1992, Vanleeuwen and Arruda 2001, Smith and Meyer 2010, Zigler et al. 2012), whereas, Wabash pigtoe are most abundant in first through third order streams (Smith and Meyer 2010, Zigler et al. 2012, Fisher 2013). Converting prairie and forest to agriculture and pasture has increased fine sediments in aquatic systems (Box and Mossa 1999). Many species are sensitive to fine sediments (e.g., pimpleback, Aldrige et al. 1987; fragile papershell, Holland-Bartels 1990) and excess fines can decrease abundances in these species and many others (Aldrige et al. 1987, McRae et al. 2004, Osterling et al. 2010). Excess fine sediment can interfere with a mussel's ability to filter feed and may result in death (Box and Mossa 1999, Cyr et al. 2012). However, some species (e.g., Wabash pigtoe) are more tolerant of fine sediments and contaminants than others (Theler 1987). Riparian corridor width (Wenger 1999, Sweeney et al. 2004) and soil erodibility (Box and Mossa 1999) both influence the amount of fine sediment entering the stream channel. Relatively small width-to-depth ratios affect bank and stream-bed stability and influence the presence of bleufer and fragile papershell

(Strayer et al. 1999, Layzer and Madison 1999, Hardison and Layzer 2001, Morales et al. 2006, Daniel and Brown 2013). In addition, relatively deep and narrow channels are linked to declines in bleufer and fragile papershell abundance (Box and Mossa 1999, Combes and Edds 2005, Gangloff and Feminella 2007). Channel sinuosity influences suspended sediment loads and velocity which can affect the availability of suitable habitat (Gordon 2004, McRae et al. 2004). Thus, we hypothesized straight channels would decrease species presence and abundance due to increased stream bed scour (Gordon 2004, McRae et al. 2004). Substrate preference has also been reported to vary among species (Cummings and Mayer 1992, Vanleeuwen and Arruda 2001), with selection influenced by shell morphology. In general, species with smooth shells are more likely to use fine substrates, whereas species with shell ornamentation or obese shells are more likely to occur in medium to coarse substrates (Watters 1994b).

We developed four competing hypotheses to predict the relative importance of habitat factors on mussel-bed presence (Table 6). The four hypotheses focused on the importance of drainage area, geology, soil, land use, riparian vegetation, and sinuosity to mussel bed presence. We hypothesized drainage area would be a primary factor influencing mussel-bed presence because it influences a variety of other abiotic factors including hydrology (Dodds et al. 2004), channel slope (Strayer 2006), and habitat availability (Atkinson et al. 2012). We hypothesized that upstream portions of our study area would be unlikely to support mussel beds because of stream drying during the summer, making it impossible for mussel beds to remain established over long temporal periods (Dodds et al. 2004, Golladay et al. 2009). Downstream portions of the rivers would have sustained base-flow conditions thereby increasing mussel survival via adequate filter feeding and reproduction (Holland-Bartels 1990, Layzer and Madison 1995, Dodds et al. 2004, Morales et al. 2006). Geology can also influence mussel-bed locations because it influences

hydrology (Strayer 2006), water quality (suspended ions- i.e., pH; Meybeck 1987), and primary substrate (Richards et al. 1996). Shale is a non-porous sedimentary rock thereby increasing run-off and discharge during precipitation events (Onda et al. 2001). We hypothesized study sites downstream of high amounts of shale would decrease mussel-bed presence due to increased erosion of the channel. We also hypothesized that stream segments where shale is the dominant geology would have fewer mussel beds because shale increases acidity of the water (Meybeck 1987). High acid levels can impair mussel growth and survival (Hincks and Mackie 1997). Soil type also influences mussel-bed presence due to erosive potential and permeability (Benbrook 1988, Bledsoe 2002). We hypothesized mussel beds were more likely to be present in areas with low soil erosion potential, because high erosion potential increase the amount of fine sediment which can smother mussel beds and create unsuitable habitats (McRae et al. 2004, Strayer 2006). Land-use practices (e.g., agriculture) also alter the amount and timing of water and sediment delivery to streams, which alters natural disturbance regimes, degrading suitable mussel-bed habitats (Box and Mossa 1999, Arbuckle and Downing 2002). We also hypothesized wider riparian corridors would be beneficial to mussel beds because of the mitigating effects of the riparian corridor to reduce bank erosion and excess sediment delivery to the channel (Wenger 1999, Sweeney et al. 2004). In addition, we hypothesized that mussel beds were more likely to occur in areas of moderate sinuosity. Straighter channels have higher stream power thereby increasing bed load that scours the stream bottom (Gordon 2004) making those areas unsuitable for mussel beds (Vaughn and Taylor 1999). Alternatively, wide and shallow channels are subject to increased solar radiation and extreme temperatures (LeBlanc et al. 1997) that reduce mussel growth (Ganser 2012) and reproductive activity (Galbraith and Vaughn 2009).

Model building and selection

Prior to model building, we standardized the data and performed preliminary diagnostic procedures. A Spearman's rank correlation procedure was completed to identify multicollinear variables. Multicollinear variables were identified using a cutoff of $r \geq 0.70$ to prevent model-estimation distortion (Smith et al. 2009, Dormann et al. 2013). When variables were highly correlated, we chose variables that were documented in the literature to have the greatest effect on species presence, species density, and mussel-bed presence. All continuous variables were tested for normality (qqplot, Shapiro-Wilk test) and transformations were made if necessary. Data were standardized by calculating the standard score ($z = \frac{X - \bar{x}}{\sigma}$; z= standard score, X= datum point, $\bar{x}$= mean of data records, σ= standard deviation) for each datum in each catchment to reduce inter-river variation. Standardizing the variables essentially gives all the variables in the dataset a mean of zero and a standard deviation of one, allowing for valid comparisons. For example, the drainage area of the Muddy Boggy was much greater than the drainage area of the Clear Boggy leading to increased variation in the data set which if not accounted for can make the results susceptible to misinterpretation. We completed diagnostic procedures using residual plots (Pearson and Deviance Statistics) to identify highly influential points or outliers. Additionally, we used Cook's distance to check for significant outliers that might influence the final model parameters.

We developed a generalized liner model (GLM) to determine which combination of habitat factors had the greatest influence on the distribution and density of four species and mussel-bed presence in the two rivers. GLM is best suited to deal with different predictors (i.e., continuous and categorical) and allows for the analysis of non-normal data. Because the dependent variable

for our presence models was binary (presence/absence), we used a binomial distribution with a logit link function. We used a negative binomial distribution for models predicting densities (count data) because there was overdispersion in our data (variance > mean; Hilbe 2011). A value of one was added to all density values because some densities were zero. All models were developed using the statistical program R (packages: lme4, GLM with AIC; bblme, AICc and Akaike weights; MASS, negative binomial distribution; AICcmodavg, AICc and model averaging; 3.1.1, R Project for Statistical Computing, New Zealand). Model structure followed the hypotheses we developed (Table 4, 5, and 6) and used presence or density as the dependent variable and hypothesized combinations of habitat factors as the independent variables. Models were compared using Akaike Information Criterion (AIC) instead of significance testing to evaluate which of our hypotheses had the most support. Smaller values reflected the least amount of information loss (information lost when approximating reality; Burnham and Anderson 2002). Because of the small sample size ($n/K<40$), AICc was used (AICc= -2(log-likelihood) + $2K$ + $2K(K+1) / n - K - 1$, where K is the number of estimable parameters and n is the number of observations; Burnham and Anderson 2002). The values produced from the models were ranked based on AICc differences (Δ_i), where Δ for model I was calculated as $\Delta_i = AICc_i - AIC_{min}$, where AIC_{min} was the smallest AICc value in the model. Based on ΔAICc values, values $\Delta< 2$ suggested substantial evidence for the model, values between 3 and 7 indicated that the model had considerably less support, and values $\Delta>10$ indicated that the model was very unlikely. For the purpose of determining the most influential models, we selected a Δ_i cutoff of < 2 as we were only concerned with identifying the variables that provided substantial support for species and mussel bed presence. Those models with the highest AICc values and $\Delta_i \leq 2$ were selected as the best models (Burnham and Anderson 2002). In addition, Akaike weights (w_i) were calculated for

each of the *r* models to create a relative weight of evidence for each model where those with the highest values represent the best models and most influential variables (Burnham and Anderson 2004). For example, an Akaike weight of 0.85 would indicate a model has an 85% chance of being selected as the top model out of the set of candidate models (Mazerolle 2004). Models that had AICc values ≤ 2 and Akaike weights < 0.90 were evaluated using model averaging ($\bar{\theta}$). Akaike weights were averaged for individual parameters and any that deviated from zero show an effect (Mazerolle 2004). Higher values indicate a greater influence in the model (Marchetti et al. 2004). Evidence ratio was determined by dividing the top Akaike weight by the next highest Akaike weight. This value indicated how much the top model was likely to be the best when compared to other candidate models (Mazerolle 2004). All of the highly ranked models were evaluated to determine how well the independent variables explained the variation of the dependent variable. We calculated the explained deviance (pseudo R^2= $100 * \frac{null\ deviance - residual\ deviance}{null\ deviance}$) where the higher the percent, the better the model (Zuur et al. 2009). Additionally, we developed box plots and scatter plots for each top-ranked model to evaluate model quality based on confidence interval (90%) overlap.

Tagging mussels

Passive integrated transponder (PIT) tags were used to individually mark mussels and evaluate how much mussels move (passively or actively) with discharge events (Figure 3). PIT tags have been widely used to study movements, habitat use, the spatial distributions of fish (Roussel et al. 2000, Riley et al. 2003, Barbin Zydlewski et al. 2005), and recently to evaluate recapture efficiency of PIT tagged mussels (Kurth et al. 2007, Wilson et al. 2011, Hale et al. 2012). Half-

duplex (HDX) PIT tags were chosen for this study because they provide greater read range and less noise distortion than full-duplex (FDX) PIT tags (Adams et al. 2006).

Previous studies have demonstrated excellent retention of PIT tags (75-100%) when the tag is attached to the outside of the mussel shell (Kurth et al. 2007, Young and Isely 2008, Wilson et al. 2011, Hale et al. 2012). Tagging followed previously established techniques by Kurth et al. (2007). A rotary tool was used to roughen and remove part of the periostracum to allow for better adherence of cyanoacrylate (dental cement). The cement was lightly applied allowing for placement of the PIT tag, which then was completely encapsulated by the cement. The cement was allowed to dry for about five minutes (dental cement had not fully cured) and then the mussel was returned to the water (Kurth et al. 2007). All PIT tags were 12 or 23-mm long, and the tag was attached to the posterior end of the left valve using dental cement (Kurth et al. 2007). The size of the PIT tag used was based on the mussel's size and weight. To not inhibit the ability of the mussel to burrow, 12-mm tags were attached to mussels with a weight < 250 g and having a small surface area (usually fragile papershell *Leptodea fragilis*, and yellow sandshell *Lampsilis teres*), whereas 23-mm tags were placed on mussels with a weight > 100 g and a large surface area (usually purple pocketbook or bleufer *Potamilus purpuratus* and threeridge *Amblema plicata*).

Several mussel species (bleufer, Wabash pigtoe *Fusconaia flava*, threeridge, fragile papershell, and yellow sandshell) were tagged in summer and autumn 2012. We chose these mussels because of their different shell types (light and smooth shells; yellow sandshell, Wabash pigtoe, and fragile papershell and heavy and ornamented or obese shells; bleufer and threeridge) and occurrence on the two rivers.

Tagging was initiated during the baseflow period (August-September 2012) to allow sufficient time after being released back into the river to burrow prior to flooding (Wilson et al. 2011). All mussels were externally tagged because of expected low mortality and high tag retention (Kurth et al. 2007, Hale et al. 2012). Juvenile mussels were excluded from tagging because they experience a decrease in burrowing rate after external tagging when compared to adult mussels (Wilson et al. 2011). Only mussels > 40 mm in length were tagged to ensure the PIT tag weight did not exceed 1% of the mussel's weight. All PIT tags had a weight < 1% of the mussel's weight, well below the recommendation of 4% to prevent altering behavior (Theuerkauf et al. 2007).

Mussels were tagged at four study sites with the goal of tagging 30 individuals at each site (~60 in each river). Kurth *et al.* (2007) reported high recaptures rates with a similar number of tagged individuals. However, we were not always able to mark 30 individuals at each site due to lower species abundance. At the time of collection, each mussel was identified, sexed if possible, weighed (g) using a portable scale (max: 5000 g), and measured with calipers (length, height and width, mm; Young and Isley 2008). After the mussels were tagged, they were returned to a 1x2-m area from where they were sampled, and a GPS point was recorded.

Additional mussels were PIT tagged in autumn (November) 2012 at the same four sampling sites in an attempt to increase the number of tagged individuals. Tagging followed the same procedure as before, but mussels were tagged using only 23 and 32 mm tags. All PIT tags had a weight < 1% of the mussel's weight, well below the recommendation of 4% (Theuerkauf et al. 2007). We increased the PIT tag size because mussels previously tagged using 12-mm tags were not relocated during subsequent resampling, presumably because they burrowed past the optimal

read range (~5-cm). Tagged mussels were released back into the same quadrat where they were sampled and a differential global positioning system (DGPS) point was recorded.

Mussel relocation

Mussels were relocated using an Oregon RFID backpack reader (Oregon RFID, Portland, Oregon, USA) during summer 2012 through autumn 2013. Resampling typically occurred every month. During winter, we sampled less often due to low flows and less movement of mussels (Allen and Vaughn 2009). A buffer area was established 20-m downstream and upstream of the mussel bed where we searched for tagged mussels. Transects were established every 2-m throughout the area, perpendicular to the direction of flow. The transects were marked using metal stakes on both sides of the river, every 2-m longitudinally throughout the buffer area. Starting from the bank, we carefully walked each transect while moving the wand (antenna for the backpack reader) slowly side to side covering an area of approximately 2 m until we reached the opposite bank. If previously marked mussels were not found within the original bed or the 20-m buffer area, an additional 20-m buffer was surveyed upstream and downstream. If, after surveying the 40-m buffer, tagged mussels were not relocated, they were assumed to have exceeded the read range or were displaced. When a mussel was relocated, its location was marked with a DGPS.

DGPS validation

DGPS validation was completed at five point locations in our study area and included each study site so we could later account for movement error due to GPS measurements. Point locations

were selected as best representing the environment encountered within the study area. One site (MB4) had two point locations because of a large distance between PIT tagged mussel areas. The validation process involved recording multiple DGPS points from a temporary point (t-post was driven into the riverbed) at each site. This information was then brought back to the lab for post-processing where we differentially corrected the points using reference stations that were in close approximation to the study sites. Once the points were corrected, they were loaded into the DGPS and then we used those coordinates to navigate back to our points. After we navigated to the specified positon using the DGPS, any distance remaining between the DGPS and the established point was measured (1.0 cm). This was completed for each coordinate position and an average was calculated for that point.

Mussel Movements

Mussel distance moved was determined after accounting for DGPS error. Mussel movements were measured using the initial PIT tag points and the associated relocation points to determine distance and direction moved. Collected DGPS points were differential corrected to increase precision of the GPS points to approximate a mussel's location. Corrected points were imported into ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA, USA) and the associated DGPS precision values were used to create a buffer around each point. If DGPS precision values were missing, the calculated validation values were used to create the buffer. Buffers were used to account for GPS error and to determine movement between points. Sampling points were only considered movements if there was no overlap in buffer areas (Frair et al. 2010). These remaining points were exported into Access (Microsoft, Redmond, WA, USA) to calculate distance between each relocation point using the associated Universal

Transverse Mercator (UTM) coordinates. Newly calculated data fields were then exported back into ArcMap.

We created an index that expressed mussel obesity (mussel shell width/length; Hornbach et al. 2010) to account for morphological differences within and among species. This index was used as a covariate in the analysis and kept in the final model if significant.

Data were analyzed as a randomized complete block repeated measures design. Site and river were used as the complete block. Site*species was the denominator of F for testing for the main effect of species. Site within species*time was the denominator of F for testing for the main effect of time and species*time. PIT-tagged mussels were treated as pseudo replicates (repeated measures). The mussel obesity index was included as a covariate in the analysis. Data were analyzed in SAS using Proc Glimmix. Fisher's protected Least Significant Difference (LSD) was used for means separation and adjusted for multiple comparisons. Discharge could not be included in the general linear mixed model (GLMM) because multiple sites used the same USGS gage data. Instead, simple linear regressions were developed between species and mean discharge at each site. Mean discharge was calculated using USGS gage data (sites 07335300, 07335000, and 07334000) and included data from each sampling event to the previous sampling event.

Results

Sidescan sonar to detect mussel beds in deep-water habitats

The optimal scanning frequency is a balance between capturing the entire stream channel bottom and obtaining high-quality image resolution. We obtained adequate detail of mussel reflectance

using high-frequency scans (down-facing beam- 200 kHz, and sidescan beam- 800 kHz). The low frequency and combination scans covered the entire stream channel in this study but we used the higher resolution images (Figure 4).

Using the captured images of mussel shells within varying substrate types, we were able to create a mussel-bed identification key based on the reflectance characteristics of the shells. Mussel shells placed in coarse substrates (i.e., pebble and cobble) were nearly impossible to identify from the surroundings substrates (Figure 5); however, we were able to easily distinguish mussel shells placed within fine substrates (i.e., sand and clay). Mussel shells were clearly visible as a cluster of white dots scattered within the fine substrate (Figure 5). Hardness and the size of the mussel shells compared to the surrounding substrate contributed to relatively clear images of the mussels. The greater hardness of the mussel shells compared to softer substrates allowed more reflectance of the sound pulse.

Overall field validations proved to be effective for locating mussel beds, but were not improved based on our potential mussel-bed classification (i.e., high, medium, low). Field validations revealed approximately 60% (10 of 17) of sites had mussel beds. However, four additional locations (approximately 25%) had living mussels, mussel shells, or both present but did not fit our definition of a mussel bed. Our qualitative classification of likelihood of finding potential mussel beds proved to be ineffective: low 56% (5 of 9 sites confirmed as a mussel bed), medium 75% (3 of 4 sites confirmed as a mussel bed), and high 50% (2 of 4 sites confirmed as a mussel bed). A mussel bed was as likely to be found in an area ranked as low potential as one ranked high potential.

Spearman's rank correlation coefficients indicated several habitat variables (58% of all possibilities) were multicollinear ($r \geq 0.30$, Table 7). Bankfull width and depth, and substrate

were highly correlated and therefore not included in the final model. Width:depth ratio (W:D) was not highly correlated with substrate so we used that combined metric to represent bankfull characteristics. Although velocity and temperature were not highly correlated with the remaining variables, they were excluded from the final model due to limited variation across sites (i.e., velocity range: 0.01-0.03 m/s, temperature range: 28-31ºC). Other retained variables were depth and sinuosity. These variables were chosen using a weight-of-evidence approach (e.g., reach scale factors are better predictors than microhabitat factors, McRae et al. 2004, Strayer 2008).

Diagnostic procedures were completed on the retained variables and the interaction of depth and velocity. Residual plots and influence statistics indicated that the same observation had a major influence on the regression parameters (deviance value was 6.95). We removed this observation and fit an additional logistic regression model. However, the new model indicated no change in significance or model fit improvement. The likelihood ratio test for the interaction term (depth*sinuosity) was not significant (P = 0.11), and therefore not included in the final model.

Our final logistic regression model indicated only one of the habitat parameters (water depth; P=0.09) was significantly related to our ability to detect mussel beds using sidescan sonar (Table 8). Our ability to accurately identify potential mussel beds was greatest at water depths of approximately 1 to 2 m (83%, 10 out of 12 sites confirmed as mussel beds), whereas our ability to accurately identify potential mussel beds decreased in the deepest areas sampled (2 to 3.4 m, 45%, 5 out of 11 sites confirmed as mussel beds). Model fit was considered to be very good based on the *c*-statistic (*c*-statistic= 0.91).

Freshwater mussel sampling

A total of 42 samples was completed at 10 sites and included 260 1-m^2 quadrats (subsamples). Twenty species were encountered (Table 9), with the downstream sites, generally, having the greatest species richness (Figure 6). Fatmucket, *Lampsilis siliquoidea,* paper pondshell *Utterbackia imbecillis*, pink papershell*, Potamilis ohiensis*, and rock pocketbook*, Arcidens confragosus* were rare, occurring at only a few sites (Table 9). Mussel densities were relatively consistent across all sites (5-7 per 1 m^2), except MB8 (3 per 1 m^2) where densities were low and MB2 (15 per 1 m^2) where densities were relatively high (Figure 7). Recruitment of juveniles into the system was evident for many species in both rivers, although more apparent in the Muddy Boggy River (Table 10).

Fish sampling near known mussel beds

We sampled a total of 2,017 fishes (Table 11). Fifty three different species were encountered representing 9 families. Highest species richness was found at the farthest downstream sampling sites (Figure 8). Fish sampling revealed 24 known fish-host species for 17 mussel species (Daniel and Brown 2013; Table 12). Fish-host abundances were greatest at the farthest downstream sampling sites (Table 13). Fishes (n = 106 fish representing 22 species) brought back to the lab to identify glochidia infection resulted in only a few confirmations. Lab examination revealed only 17 fish were confirmed to be infected. Confirmed species in declining frequency of infection were channel catfish *Ictalurus punctatus* (n= 6), blacktail shiner *Cyprinella venusta* (n= 3), bluegill *Lepomis macrochirus* (n= 2), longnose gar *Lepisosteus osseus* (n= 2), largemouth bass *Micropterus salmoides*(n= 1), longear sunfish *L. megalo*tis (n=1), black redhorse *Moxostoma duquesni*, (n= 1), and common carp *Cyprinus carpio* (n= 1).

There was a positive relation between mussel densities and fish-host abundance (log transformed) for two of the four mussel species. Freshwater drum *Aplodinotus grunniens* abundance was positively related to bleufer densities (F= 4.14, p <0.10, R^2= 0.41) and fragile papershell densities (F= 5.01, p<0.10, R^2= 0.46; Figure 9). Fish-host abundance was not significantly related to increases in pimpleback *Quadrula pustulosa* (F= 0.44, p= 0.53, R^2= 0.07) or Wabash pigtoe densities (F= 0.05, p= 0.83, R^2= 0.01; Figure 9).

Influence statistics and correlations

Spearman's rank correlation coefficients for presence data indicated only a few landscape factors (11%, three of 28) were multicollinear ($r \geq 0.70$, Table 14). Riparian corridor width, proportion of agriculture and pasture land, and proportion of forested vegetation were all multicollinear. Proportion of agriculture and pasture land was negatively correlated with riparian corridor width, whereas proportion of forest was positively related. As expected, proportion of forest and proportion of agriculture and pasture land were significantly negatively correlated.

Spearman's rank correlation coefficients for species density and habitat data indicated over a third of the factors (36%, 10 out of 28) were multicollinear ($r \geq 0.70$, Table 15). Density correlations also indicated highly erodible land, width-to-depth ratios, and geology were highly correlated. Land use was multicollinear with all variables except sinuosity. Drainage area was negatively correlated with highly erodible land and land use.

Residual plots and influence statistics did not indicate any significant deviations when evaluated for all the models. Therefore, no changes were made to improve model fit. Cook's distance test identified a few data points as outliers, however, data points were checked for errors (none were found) and retained.

Models predicting mussel bed and species presence

Three of the four GLM models predicting mussel-bed presence had substantial support via AICc model ranking (Table 16). The top model (M1, ΔAICc = 0, w_i = 0.32) indicated mussel beds were more likely to occur downstream (drainage area: $\bar{x}$ = 3,668 km^2, SD= 2,192) and in areas where agriculture and pasture land were limited (Land: $\bar{x}$= 17%, SD = 20). Model averaging indicated drainage area and agriculture and pasture land had nearly the same influence in the model ($\bar{\theta}$= 0.22 and 0.21, respectively). The second top model (M4, ΔAICc = 0.05, w_i = 0.31) included the same parameters but with the addition of locations where soil was more resistant to erosion (HEL: $\bar{x}$ = 42%, SD= 5). Model averaging indicated that HEL ($\bar{\theta}$= 0.57) was more influential than drainage area ($\bar{\theta}$= 0.22) and the proportion of agriculture and pasture land ($\bar{\theta}$= 0.21), because it had a greater separation from zero than the other variables. Lastly, the third top model (M2, ΔAICc = 0.25, w_i = 0.28) indicated mussel beds were more likely to occur in areas with a wide riparian corridor (Rip: $\bar{x}$= 139.11 m, SD = 42.06) and where both soil and bank composition were resistant to erosion (87%, 20 out of 23 identified as resistant banks). Model averaging indicated that HEL ($\bar{\theta}$= 0.57) was more influential in the model than riparian corridor width ($\bar{\theta}$= 0.01). Akaike weight suggested, given our data, our top model had a 32% chance of being selected as the top model of the candidate models. The Akaike weights of the other two top models had a 31% and 28% chance of being selected. The evidence ratio indicated the top model was very unlikely to perform better than the other two models (1.03 and 1.14 times more likely). The explained deviance values indicated that, while model 3 was the better of the top AIC models, it explained very little variation (12%) in mussel bed presence. Box plots showed a

substantial amount of overlap of the confidence intervals suggesting these models were, in general, poor predictors of mussel-bed presence.

Results from the AICc model ranking indicated several variables were influential to multiple species (Table 17). Drainage area was considered highly influential in 67% (four of six) of the top ranked species presence models. In 75% (three of four) of these models, species were more likely to be found in the downstream reaches of the rivers, whereas one species, Wabash pigtoe, occurred most often in upstream reaches. Riparian corridor width often co-occurred in influential models with drainage area or agriculture and pasture land. Contrary to our hypothesis, fragile papershell was more likely to occur in downstream areas in areas with wider riparian corridors, whereas Wabash pigtoe occurred in areas of increasing agriculture or pasture lands and narrower riparian corridor width.

For three of the mussel species, there was only substantial support for one hypothesis but only one species model was a good predictor of species presence. The highly supported model predicting bleufer presence included drainage area and width-to-depth ratio (M2, ΔAICc = 0, w_i = 0.70). Bleufer was most likely to occur in downstream reaches (drainage area: $\bar{x}$ = 2,360 km^2, SD= 1,765), and in channels with moderate width-to-depth ratios (WD: $\bar{x}$= 23.67, SD = 4.64). Model averaging indicated that width-to-depth ratio ($\bar{\theta}$= 1.59) was only slightly more influential than drainage area ($\bar{\theta}$= 1.34). Akaike weight suggested, given our data, this variable combination had a 70% chance of being selected as the top model of the candidate models provided. However, the explained deviance and box plots (some overlap of the confidence intervals) indicated the model was only fair at predicting bleufer presence (pseudo R^2= 30%). The top ranked model predicting fragile papershell presence included drainage area and riparian corridor width (M1, ΔAICc = 0, w_i = 0.78). Fragile papershell was most likely to occur downstream

(drainage area: $\bar{x}$ = 2,247 km^2, SD= 1793), and in areas with a relatively wide riparian corridor (Rip: $\bar{x}$= 123.6 m, SD = 47.44). Model averaging indicated that drainage area ($\bar{\theta}$= 1.65) was only slightly more influential than riparian corridor width ($\bar{\theta}$= 1.32), but Akaike weight suggested the top model had a 78% chance of being selected. Again, the explained deviance and box plots suggested the model was rather poor at predicting fragile papershell presence (pseudo R^2= 21%). The highly supported model predicting Wabash pigtoe presence included riparian corridor width and proportion of agriculture and pasture lands (M3, ΔAICc = 0, w_i = 0.94). Wabash pigtoe occurred in areas with narrower riparian corridors ($\bar{x}$= 116 m) when compared to absent locations ($\bar{x}$= 138 m). Wabash pigtoe also occurred in areas with moderate proportions of agriculture and pasture land use (Land: $\bar{x}$= 23%, SD = 25). Model averaging indicated that both variables had a similar influence (riparian corridor width $\bar{\theta}$= 3.89 and land use $\bar{\theta}$= 3.69) on mussels, but Akaike weight suggested the top model had a 94% chance of being selected. Unlike previous models, the explained deviance and box plots indicated the model was adequate at predicting Wabash pigtoe presence (pseudo R^2= 36%).

Model ranking suggested there was substantial support for multiple hypotheses for predicting pimpleback presence. The top ranked model predicting pimpleback presence only included drainage area (M1, ΔAICc = 0, w_i = 0.45). Pimpleback was most likely to occur in downstream reaches (drainage area: $\bar{x}$ = 2,298 km^2, SD= 1903). The second ranked model (M4, ΔAICc = 0.91, w_i = 0.28) indicated pimpleback was most likely to occur downstream, in areas where soil (HEL: $\bar{x}$ = 41%, SD= 6) and river banks (90%, 10 of 11 identified as resistant) were more resistant to erosion. Model averaging indicated that drainage area ($\bar{\theta}$= 0.75) was most influential in the model when compared to HEL ($\bar{\theta}$= 0.07). The third ranked model (M2, ΔAICc = 1.19, w_i = 0.25) indicated pimpleback was most likely to occur in portions of the river where there was a

decrease in both shale (Geo: $\bar{x}$ = 29%, SD= 23) and forested vegetation (Forest: $\bar{x}$ = 61%, SD= 21). Model averaging indicated that shale ($\bar{\theta}$= 0.87) was only slightly more influential in the model than forest cover ($\bar{\theta}$= 0.67). Akaike weight suggested, given our data, our top model had a 45% chance of being selected as the top model of the candidate models. The Akaike weights of the other models (M4 and M2) had a 28% and 25% of being selected, respectively. The evidence ratio suggested the top model was only 1.61 and 1.80 times more likely than the other two models to be the best. The explained deviance values indicated that model 4 was the better model but only explained 20% of the variation in pimpleback presence (M4, pseudo R^2= 20%; M2, pseudo R^2=14%; M1, pseudo R^2=6%). Box plots suggested the top models were not adequate at predicting pimpleback presence.

Models predicting species densities

Results from the AICc model ranking indicated several variables were influential to multiple species densities (Table 18). Drainage area, width-to-depth ratio, and proportion of shale geology were selected most often, occurring in 83% (five of six) of the top ranked models. Models for all species except Wabash pigtoe included drainage area as a top variable. Species densities were highest in the downstream reaches of the study area.

Model ranking indicated a few variables were species specific. Proportion of shale and width-to-depth ratio were influential variables in the top models for bleufer and fragile papershell. Both species had higher densities in areas with low proportions of shale geology and moderate width-to-depth ratios. A high proportion of agriculture and pasture land use was positively related to increasing Wabash pigtoe densities. Bleufer densities were highest in areas with the widest riparian corridor and predominately moderate to coarse substrates.

Model ranking suggested there was substantial support for multiple hypotheses for two species. AICc model ranking for bleufer (M2, ΔAICc = 0, w_i = 0.36; M1, ΔAICc = 0.17, w_i = 0.33; M3, ΔAICc = 0.33, w_i = 0.31) and fragile papershell (M2, ΔAICc = 0, w_i = 0.37; M1, ΔAICc = 0.15, w_i = 0.35; M3, ΔAICc = 0.63, w_i = 0.27) indicated that there was substantial support for three of the four hypothesized models. Bleufer densities were highest downstream (highest density where drainage area was 5,860 km^2), whereas lower densities occurred throughout the other study sites (Figure 10). Further, the highest bleufer densities were associated with the widest riparian corridor (196 m), but lower densities occurred over a range of riparian corridor widths (43-167 m; Figure 10). The highest densities of bleufers occurred where width-to-depth ratios were moderate (22-26; Figure 10). Additionally, sites with < 50% shale and predominately moderate to coarse substrates also had the highest densities which may reflect flow stability at that site rather than a preference for substrate. Results from the two top models suggested drainage area ($\bar{\theta}$= 0.28, 0.35, respectively) was slightly more influential than width-to-depth ratios ($\bar{\theta}$= 0.18) or riparian corridor width ($\bar{\theta}$= 0.03). Akaike weight suggested that the chance of being selected as the top model was similar among the three models (36%, 33%, and 31%, respectively). The evidence ratio indicated the top model was only 1.09 and 1.16 times more likely than the other two models to be the best. The explained deviance values indicated that model 2 was the better model and explained 28% of the variation in bleufer density (M2, pseudo R^2= 28%; M1, pseudo R^2=22%; M3, pseudo R^2=17%). Fragile papershell densities were highest downstream (drainage area of 5,813 km^2, Figure 11). The highest densities of fragile papershell occurred where width-to-depth ratios were moderate (22-24; Figure 11) and percent shale was relatively low (11%-45%; Figure 11). Results from the top two models suggested shale ($\bar{\theta}$= 0.66, 0.74, respectively) was slightly more influential than width-to-depth ratios ($\bar{\theta}$= 0.57) or

drainage area ($\bar{\theta}$= 0.05). Results from the third top model suggested drainage area ($\bar{\theta}$= 0.52) was more influential than width-to-depth ratios ($\bar{\theta}$= 0.17). Akaike weight suggested that the chance of being selected as the top model was similar among the three models (37%, 35%, and 27%, respectively). The evidence ratio indicated the top model was only 1.06 and 1.37 times more likely than the other two models to be the best. The explained deviance values indicated that model 2 was the better model and explained 46% of the variation in fragile papershell density (M2, pseudo R^2= 46%; M1, pseudo R^2=44%; M2, pseudo R^2=36%).

Model ranking indicated there was substantial support for only one model predicting pimpleback density (M1, ΔAICc = 0, w_i = 0.88) and one model predicting Wabash pigtoe density (M1, ΔAICc = 0, w_i= 0.94). Pimpleback density was greatest in the downstream portion of the study area (drainage area= 5,813 km^2, Figure 12). Akaike weight suggested there was a 70% chance of this model being selected as the top model of the candidate models and the explained deviance and scatter plot suggested model fit was good (pseudo R^2= 39%).Wabash pigtoe densities were exceptionally high in areas with relatively high agriculture and pasture land use (66%-73%; Figure 13). Akaike weight suggested there was a 94% chance of this model being selected as the top model of the candidate models and the explained deviance and scatter plot indicated model fit was very good (pseudo R^2= 65%).

Mussel movements

Five different species of mussels were PIT tagged at four sites. We PIT tagged more bleufer as it was the most frequently encountered, particularly at both downstream study sites (Table 19). We tagged fewer Wabash pigtoe than other species; however, it was fairly abundant at the upstream sampling site on the Clear Boggy River.

PIT-tagged mussels were relocated on nine different occasions and included approximately 2000 relocation points. Mussel recapture rates ranged from 29% to 89%, with lower recaptures occurring during winter when mussels burrowed and higher recapture rates occurring during summer when mussels were at the surface. Time steps one (Sept 2012) and two (Nov 2012) were omitted from the analyses to allow redistributions at the study sites during and following tagging. Time steps four (May 2013) and five (June 2013) had to be omitted due to low recapture rates during those periods, primarily associated with fragile papershell (e.g., only 1 detection at MB4 during May).

Validation of the DGPS to identify the precision to measure back to a specific point varied between ~10 and ~200 cm, with a mean of ~115 cm. The precision of the DGPS was influenced by dense tree canopy and steep and narrow river channels.

The GLM used to assess differences in mussel movements was fit using an index for obesity as a covariate. The index was significant in the model ($F_{1,850} = 7.59$, $P < 0.01$). After taking the index into account, there were no significant differences in movement between species ($F_{4,10} = 1.48$, $P = 0.28$). However, movement of freshwater mussels was significantly different with time ($F_{4,51} = 17.18$, $P < 0.01$) but the time*species interaction was not significant suggesting differences in movement with time did not depend on species ($F_{16,51} = 1.20$, $P < 0.30$). Mussel movement was greatest during time step three (3.78 m), similar during time steps 6-8, then declined to the lowest value at time step nine (0.90 m) (Figure 14). These results correspond with the life-history of the species suggesting movements are greatest when preparing for phases of the reproductive period.

Simple linear regressions between mussel movements and mean discharge (between the sampling event and the preceding sample event) suggested that, in general, mussel movement

was not related to discharge. Only fragile papershell showed a positive relationship between movement and discharge ($F_{1,9}$=4.64, Adj R^2=0.27, P=0.06) and only at one site (CB5; Figure 15). However, one datum is pulling the direction of the relationship so this result should be interpreted with caution.

Discussion and recommendations

Sidescan sonar

We have shown that sidescan sonar can be a useful tool for assessing potential freshwater mussel beds over a broad area and under environmental conditions where traditional sampling may be difficult or impossible. This is one of the first studies that we are aware of that used an inexpensive sidescan sonar system in a river to locate freshwater mussel beds. Our results are similar to a study that used a large and expensive sidescan sonar unit with towfish to accurately map (~80%) zebra mussel *Dreissena polymorpha* coverage on substrate in Lake Erie (Haltuch et al. 2000). However, some refinement would be helpful to improve detection. For example, our ability to accurately identify mussel beds diminished at water depths greater than 2 m. We hypothesize this may be caused by how the sidescan sonar sound signal is reflected from the mussel shells due to incident angle. In shallow-water habitat, the signal is more likely to be reflected at a horizontal path, whereas in deeper water the signal would travel a more oblique path such that much of the reflected energy is directed away from the transducer. Several of the potential mussel bed areas identified during field validation were deep pools with silt substrates. Silt sediments can degrade image quality due to a loss in energy of backscatter (Degraer et al. 2003, Dartnell and Gardner 2004, Collier and Brown 2005), and this was an issue we also

encountered when creating our reference images in silt substrates (~90%). Additionally, deeper pools typically have homogeneous substrates; however, isolated amounts of coarse substrates may appear as mussel reflectance increasing false-positive results. Our reference images developed under relatively homogenous conditions in a reservoir suggest substrate is a major factor to detecting mussels; however, W:D ratios (highly correlated with dominant substrate) was not a good predictor of mussel presence under riverine conditions. Increased heterogeneity within the river channel is a probable reason why riverine factors were more difficult to determine with our logistic regression model. We suggest more intense habitat mapping (e.g., substrate at each 1-m area scanned rather than dominant substrate across a channel unit) would provide more insight. Other physical factors that we did not measure may also be important determinants of useful sidescan sonar images (e.g., woody debris, microhabitat substrate mapping, suspended sediment).

Sidescan sonar can help managers safely locate freshwater mussels over extensive areas that may be too difficult or dangerous to sample using traditional techniques. Traditional sampling for freshwater mussels involves intensive visual and tactical searches of an aquatic system (Miller and Payne 1993, Beasley and Roberts 1996, Hastie and Cosgrove 2002). In some cases, only certain habitat areas are sampled in an attempt to target habitats perceived to be suitable for mussels (Metcalfe-Smith et al. 2000). Additionally, some areas are targeted because ease of sampling over other habitats (Smith et al. 2003). Traditional mussel sampling can be difficult if not impossible in systems that are deep and turbid (Isom and Gooch 1986). Visual searches cannot be performed in very turbid water and instead, the investigator must rely on tactile searches to locate mussels. In deep-water systems, SCUBA may be required and multiple divers needed to ensure safety (Isom and Gooch 1986, Metcalfe-Smith et al. 2000). Sidescan sonar

could be a helpful tool to allow a cursory examination of hazardous areas without needing to spend much time in the water. Follow-up sampling can then be used to target locations where mussels are likely to occur to gain information on assemblage structure and population dynamics.

Using a tool to target intensive sampling locations can be useful when directing limited resources. In our study, a two-person team could survey a 32-km reach with sidescan sonar in approximately 5 h (~ 6.5 km per hour), whereas labor intensive field sampling of an area of similar size (34 km) can take 47 person days (0.09 km per hour) to complete (Christian and Harris 2005a). Although time spent in the field using sidescan sonar is substantially less when compared to traditional sampling, processing the sonar data took an additional 40 to 60 h (~1.5 hours per km); however, user experience can substantially decrease this time. These times vary depending on habitat conditions and the speed traveled when sonar data are collected. In addition, sidescan sonar can be used to gain a general idea about substrate size and location of major underwater structure within a reach (Kaeser and Litts 2008, Kaeser et al. 2012) which may be helpful when evaluating mussel-bed distributions. Quickly identifying underwater habitats associated with mussel beds allows less time in the field and more insight into potential environmental influences.

Sidescan sonar provides an inexpensive and effective method for locating freshwater mussels, though its application is limited. The sidescan sonar unit we used in this study cost approximately US $2000, substantially less when compared to other sidescan units used for benthic mapping (Klein 595, ~ US $20,000, www.l-3mps.com, Hewitt et al., 2004; CM 800, ~ US $26,000, www.cmaxsonar.com, Hartstein, 2005; EdgeTech 4100, ~ US $40,000, www.edgetech.com, Teixeira et al., 2013; Accessed March 31, 2014). Our ability to identify

freshwater mussel beds using sidescan sonar was promising but also limited to moderate depths (1-2 m). We could improve our ability to detect mussels in deeper water by incorporating a towfish. There is readily available information about how the transducer can be modified into a towfish (e.g., http://forums.sideimagingsoft.com, http://bb.sideimageforums.com). Additionally, adding the transducer to a longer pole may allow for better image quality by reducing water depth between the transducer and the benthos. Further, times of year and discharge conditions during sampling are additional limitations. Many freshwater mussels remain beneath the substrate surface during winter months (Allen and Vaughn 2009) making this period ineffective for locating mussel beds. Sampling during the reproductive cycle when adults are exposed above the substrate surface provides the best opportunity to capture sonar images of a mussel bed. Sampling during elevated-discharge conditions during the early tachytictic reproductive period (late spring, early summer; Graf & Foighil, 2000; Galbraith & Vaughn, 2009) would enable image capture of the entire channel in a single survey during ideal navigation conditions (Kaeser and Litts 2010, Kaeser et al. 2012). Sidescan sonar surveys during low-flow periods of the bradytictic reproductive cycle (late summer) would result in difficult and increased image distortion in shallow water.

Taking the proper steps to refine sonar image capture quality will improve the clarity and reliability of sidescan sonar images while improving the probability of mussel-bed detection. First, frequency settings may need to be adjusted for different bodies of water. A high frequency of 800 kHz provides for the greatest resolution for image capture, but can limit stream width captured by a single image (~35 m for the current study). Wider streams may require a lower frequency to capture bank to bank images but the resolution of the data would be reduced. Kaeser et al. (2012) reported that a frequency of 455 kHz allowed for image capture of a stream

up to 98-m wide (49 m on each side of the transducer). Sampling wider streams, while maintaining adequate image detail, would likely require two complete passes to adequately capture images of each bank. Multiple sidescan sonar surveys would also allow for cross comparison among recorded sonar images. Comparisons among multiple sidescan images can help validate potential mussel-bed locations if the same mussel bed is present in multiple images even when habitat conditions have changed.

We provided initial reference images for other investigators; however, more images would be helpful under controlled environmental conditions. In particular, we suggest developing a series of reference images to distinguish shell characteristics in more heterogeneous habitats. We found we could clearly identify mussel shells in homogenous fine substrates (excluding fine sediment), which agrees with Haltuch et al. (2000), but our commission errors likely resulted from some coarse substrates at misidentified sites. One possible way to improve detections would be to conduct multiple scans such as during winter when mussels are beneath the substrates and then re-scan when mussels emerge for reproduction and assess images for discrepancies. This might provide a helpful approach as long as major floods have not reworked the alluvium between scans. Additionally, multiple sidescan sonar surveys of a study area over a short period of time would likely improve detection accuracy. We anticipate the refinements made by sampling multiple passes over multiple seasons will increase the accuracy of detecting mussels in turbid environments making sidescan sonar more broadly applicable to freshwater environments.

Distribution and abundance of mussels

The models we developed to predict mussel densities were often better fits to our data than those developed to predict mussel-bed and species presence (an exception is Wabash pigtoe presence).

One explanation may relate to how we defined a mussel bed. Mussels were generally lower in abundance in the mussel beds we sampled when compared to other studies. Christian and Harris (2005) considered a large mussel bed as an area where mussel density >10 per m^2 and covering >500 m^2. We considered a mussel bed with a density of >5 per m^2 and covering 300 m^2 to be very large. Our mussel presence hypotheses may not have predicted well because of the differences in the character of the rivers where information was obtained for hypotheses development. Some of the evidence we used came from clear stream systems in different geographic regions where influential factors may be different (Howard and Cuffey 2003, McRae et al. 2004, Strayer 2006). Another possibility could be related to limited variation in presence across each river, with many species occurring at both upstream and downstream study sites. The species that showed the strongest relationships were those that demonstrated obvious longitudinal preferences (e.g., Wabash pigtoe) This was also true for our models predicting mussel densities where the best fit occurred via species that had much higher densities at some sites (rather than occurring at low densities throughout). Lastly, bed locations may be related to other abiotic factors either not measured in our study (e.g., shear stress, Daraio et al. 2010; bed stability, French and Ackerman 2014) or biotic factors (Schwalb et al. 2013) that were not accounted for in the models because fish were not sampled at all of the bed locations. Further, low adult mussel densities or uneven sex ratios may also result in low numbers of gravid females and few infections of fish hosts (Jones and Neves 2011; Arvidsson et al. 2012).

Drainage area was included in 65% (11 of 17) of the top models predicting species or mussel-bed presence or densities of mussels. Drainage area is related to the availability of different habitats and changes in some ecosystem components are predictable with increases in drainage area or stream size (Vannote et al. 1980). Drainage area is an important factor

influencing freshwater mussel distributions (Strayer 2006, Atkinson et al. 2012). Atkinson et al. (2012) found that stream size influenced the longitudinal position of many mussel communities and that there was a predictable shift in community composition with distance downstream from the headwaters. More often, mussels found in headwaters are smaller and short lived, while species downstream are larger and longer lived, likely because of the greater environmental variability exhibited in the headwaters (Atkinson et al. 2012, Haag 2012). For example, we found that bleufer, a long-lived and large species, had greater densities downstream, whereas, Wabash pigtoe, a smaller and shorter-lived species had greater densities upstream. Further, habitats exhibiting greater bed stability (i.e., downstream) are more likely to have increased species occurrences and survivorship (Widdows et al. 2002, Atkinson et al. 2012).

The importance of downstream areas for mussels could be related to three abiotic factors: stream drying (Gough et al. 2012), hydrology (Widdows et al. 2002), and water temperature (Archambault et al. 2014, Daraio et al. 2014). Stream drying likely limits persistence of mussels in the upstream portions of these rivers because mussels have limited mobility making it difficult to escape harsh drying conditions (Gough et al. 2012). Likely, only a few species that have specific traits to deal with these spates can survive (Galbraith et al. 2010). Additionally, downstream areas are more likely to have greater flow stability allowing for mussel-bed establishment and persistence (Widdows et al. 2002) and reduces species displacement (Schwendel et al. 2010). Headwaters that are prone to stream drying and have increased amounts of agriculture land use are also more likely to have greater variability in water temperatures (Archambault et al. 2014, Daraio et al. 2014). Both of our study rivers have dry sections in the upstream river portions and agriculture land use in the headwaters, which likely related to decreased presence of species that are intolerant of extreme temperature fluctuations.

Fish-host presence was anticipated to be an important factor influencing mussel distributions (Vaughn and Taylor 2000, Schwalb et al. 2012, Daniel and Brown 2013), but some mussel species were more sensitive to the presence or abundance of fish host than others. We found that densities of two mussel species, bleufer and fragile papershell, were positively related to increased abundance of their host fish; however, two other mussel species, pimpleback and Wabash pigtoe, showed no significant relationship with host abundance. The increase in density by the two mussel species was likely because they each only have one fish host making this biotic factor much more important than it might be for other species with multiple hosts (Daniel and Brown 2013). Increases in the number of host fish would increase reproductive success and influence the distribution of species (Daniel and Brown 2013). After glochidia (mussel larvae) attach to the gills or fins of their host fish, they remain attached for three to four weeks before they release from the host (Watters 1994a). If they are released in suitable habitat, they are likely to survive to increase the density of existing beds or create new ones (Watters 1994a, Daraio et al. 2010, Schwalb et al. 2011). Daniel and Brown (2013) and Schwalb et al. (2013) found that mussel species presence and density were highly influenced by fish-host presence, and that this was even more apparent when mussel species had a limited number of host fish. Our results, however, should be interpreted with caution because our limited sampling supported only a limited scope of analyses. Future research would benefit from increasing the number of study sites to examine the influence of fish hosts on mussel presence.

The density models for fragile papershell, pimpleback, and Wasbash pigtoe were also considered good predictors (i.e., little overlap in confidence intervals). Fragile papershell and pimpleback both included drainage area in one or more of their tops models. This agrees with other studies that have found distance from the headwaters to be significantly related to fragile

papershell and pimpleback presence (Cummings and Mayer 1992, Vanleeuwen and Arruda 2001, Smith and Meyer 2010, Zigler et al. 2012, Fisher 2013). Pimpleback densities appeared to be driven more by drainage area in the Muddy Boggy than in the Clear Boggy. However, unlike pimpleback densities that were most influenced by drainage area, fragile papershells were also negatively related to shale geology and positively related to moderate width-to-depth ratios. Fragile papershells are sensitive to water-quality degradation, including increases in heavy metals (Milam et al. 2005, March et al. 2007). No formal studies have been conducted to evaluate the effects of pH increases on fragile papershell; however, increased percent shale geology would increase pH levels (Meybeck 1987) and that could be problematic for fragile papershells because their thin shells may be negatively affected (i.e., inhibit shell development or dissolve the calcium in the shell) by higher acidity levels in the water (Watters 1994b). Combes and Edds (2005) and Zigler et al. (2012) found that fragile papershells typically occurred in areas of moderate width-to-depth ratios. Moderate levels of width-to-depth ratios typically relate to greater flow stability (Rosgen 1994). The top-ranked model predicting Wabash pigtoe densities, reinforcing our hypotheses of a positive relationship between densities and modified lands, was the best model when compared to all species models (R^2= 0.65). Wabash pigtoes are more tolerant of fine sediment inputs (Nakato et al. 2007) and are better able to cope with hydrologic variability caused by land-use practices than species like fragile papershell and pimpleback (Van Der Schalie and Van Der Schalie 1950, Buchanan 1980, Theler 1987).

The models predicting bleufer densities were inadequate and may be due to limited published information on the factors that most influence their occurrence. The majority of published literature on bleufer focuses on one or two factors (i.e., drainage area, substrate composition) that influence presence (Miller and Payne 2001, Combes and Edds 2005, Tiemann et al. 2011a).

Drainage area was included in the most influential models and was positively related to bleufer densities, confirming what others have reported (Miller and Payne 2001, Combes and Edds 2005). Other variables (i.e., riparian corridor width, proportion of shale) that were included in the models were based on published literature that evaluated general mussel distributions and were not specific to one species (Wenger 1999, Arbuckle and Downing 2002). Future exploratory studies on factors influencing bleufer densities would increase our understanding of their distributions.

Whereas we did not measure water quality directly, it can influence mussel occurrences (Watters 1999, Shea et al. 2013, Zipper et al. 2014) and can be affected by some land-use practices. For example, agriculture and pasture land use influence the quantity of fine sediment in the stream channel (Box and Mossa 1999) and if in excess, can smother mussels (Ten Brinke et al. 1995, Henley et al. 2000). We found increases in highly erodible soils and agriculture and pasture land use to occur together in models suggesting the presence of erodible soils in agriculture and pasture regions may limit some species (e.g., bleufer and pimpleback). Soils that are more susceptible to erosion will increase in-channel sediment likely decreasing water quality for mussel communities (Waters 1995, Box and Mossa 1999). However, increased riparian corridors appear to negate some of the influence of agriculture and pasture land use allowing persistence of mussel populations in these areas. In most cases, as riparian corridor width decreases so do many aquatic organisms including freshwater mussels (Wenger 1999, Pusey and Arthington 2003). Wenger (1999) found that fish and invertebrate diversity declined when riparian corridor width was < 30-m wide. Wide riparian corridors have a greater capacity to buffer fine sediment inputs (Wenger 1999, Sweeney et al. 2004). Additionally, riparian zones increase bank stability thereby reducing bank erosion and collapse (Sweeney et al. 2004, Piégay

et al. 2005). Excess nutrients and chemicals may be released into a stream due to increased erosion which adversely affects mussels. Miller et al. (2014) found that stream banks with greater amounts of riparian vegetation were better at buffering against stream bank erosion and decreasing the amount of water soluble phosphorus entering the water system. Riparian corridors also help to buffer against agriculture contaminants like pesticides and fertilizers that negatively affect mussels (Poole and Downing 2004, Anbumozhi et al. 2005). Wenger (1999) suggested riparian corridors of 30-100 m wide would adequately control sediment and provide optimal habitat and buffering capacity in most streams.

Increasing our knowledge about the distribution of freshwater mussels and the influence of environmental factors is important to developing effective conservation efforts. A current conservation focus is on propagation and reintroduction or introduction of mussels into streams and rivers. Unfortunately, only half of the current reintroductions or introductions of mussels into an aquatic system that have been evaluated are successful (Cope and Waller 1995, Peck et al. 2007). The lack of success may be related to several factors including *a priori* evaluation of suitable habitat conditions at multiple spatial scales (Cope and Waller 1995, Peck et al. 2007). The results of our study provide information on what environmental factors are most likely to influence specific-species densities, which can guide conservation initiatives. This research could help managers decide what areas or species may be most suitable for reintroductions. For example, if managers want to reintroduce mussels into a river system influenced by an agricultural landscape, stream segments offering wide riparian corridors (> 30 m) would be preferable. More importantly, selecting a more tolerant species would be appropriate and our research suggests Wabash pigtoe to be a likely candidate for river systems draining agriculture and pasture land use. There appear to be no significant differences between movements of the

species we PIT tagged but there are obvious longitudinal preferences as some species show an ability to tolerate the threats at some locations better than others. However, our movement objective was hindered by the general low densities of the mussels at various sites.

This study provides insight into the factors that are likely to influence mussel presence and densities, but additional studies would be beneficial. First, many recent studies (e.g., juvenile mussel presence, Daraio et al. 2010, French and Ackerman 2014; mussel presence, Daniel and Brown 2013, Davis et al. 2013) have found relationships between presence and channel slope or shear stress, particularly for the juvenile life stage (e.g., *Epioblasma triquertra, Villosa iris, Lampsilis fasciloa,* and *Ligumia nasuta,* French and Ackerman 2014). Increased shear stress is associated with decreased bed stability and requires additional energy output by mussels to maintain position and filter feeding (Rempel et al. 2000, French and Ackerman 2014). However, several mussel species are able to tolerate elevated shear stress. For example, species with shell ornamentation (e.g., washboard, *Megalonaias nervosa*; threeridge, *Amblema plicata*) are more likely to avoid downstream displacement when compared to those species with smooth shells (e.g., fragile papershell; yellow sandshell, Watters 1994b, Allen and Vaughn 2009, Hornbach et al. 2010). Developing a hydraulic model that can predict shear stress under a range of discharge conditions would provide important information about possible species displacement at high flows. It would also be important in identifying flow refuges within rivers where reintroductions would be likely to be more successful. Lastly, expanding studies to include multiple catchments would benefit our understanding of the relationship among landscape factors and the persistence of mussel populations.

Acknowledgements

This research was supported by the Oklahoma Department of Wildlife Conservation and was conducted under the auspices of the Oklahoma State University Animal Care and Use Committee (ACUP AG1218). Special thanks to Thomas Campbell, Daniel Beatie, Mark Jensen, and Bryce Burkehead for field and laboratory assistance. We thank Megan Bradburn and David Martinez for thoughtful comments on an earlier draft. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

III. RECOMMENDATIONS

Management recommendations are provided above in the discussion and recommendations section.

IV. SIGNIFICANT DEVIATIONS

No significant deviations.

V. EQUIPMENT

No equipment purchased during this period.

VI. PREPARED BY:

Shannon Brewer and Jarrod Powers
Oklahoma Cooperative Fish and Wildlife Research Unit,
Oklahoma State University Stillwater, Oklahoma

DATE: 17 February 2015

APPROVED BY: _____

Fisheries Division Administration
Oklahoma Department of Wildlife Conservation

_____

Andrea Crews, Federal Aid Coordinator
Oklahoma Department of Wildlife Conservation

VI. REFERENCES

Adams, A., R. K. Wolfe, W. Pine, and B. Thornton. 2006. Efficacy of PIT tags and an autonomous antenna system to study the juvenile life stage of an estuarine-dependent fish. Estuaries and Coasts 29:311-317.

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

Allen, D. C. and C. C. Vaughn. 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. Journal of the North American Benthological Society 28:93-100.

Allen, D. C. and C. C. Vaughn. 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. Journal of the North American Benthological Society 29:383-394.

Allison, P. 1999. Logistic regression using the SAS System. SAS Institute. Inc., Cary, NC.

Anbumozhi, V., J. Radhakrishnan, and E. Yamaji. 2005. Impact of riparian buffer zones on water quality and associated management considerations. Ecological Engineering 24:517-523.

Arbuckle, K. E. and J. A. Downing. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Canadian Journal of Fisheries and Aquatic Sciences 59:310-316.

Archambault, J. M., W. G. Cope, and T. J. Kwak. 2014. Survival and behaviour of juvenile unionid mussels exposed to thermal stress and dewatering in the presence of a sediment temperature gradient. Freshwater Biology 59:601-613.

Atkinson, C. L., J. P. Julian, and C. C. Vaughn. 2012. Scale-dependent longitudinal patterns in mussel communities. Freshwater Biology 57:2272-2284.

Arvidsson, B. L., J. Karlsson, et al. 2012. Recruitment of the threatened mussel *Margaritifera margaritifera* in relation to mussel population size, mussel density and host density. Aquatic Conservation: Marine and Freshwater Ecosystems 22: 526-532.

Barbin Zydlewski, G., A. Haro, K. G. Whalen, and S. D. McCormick. 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. Journal of Fish Biology 58:1471-1475.

Beasley, C. R. & D. Roberts. 1996. The current distribution and status of the freshwater pearl mussel *Margaritifera margaritifera* L 1758 in north-west Ireland. Aquatic Conservation-Marine and Freshwater Ecosystems 6: 169-177.

Benbrook, C. M. 1988. First principles - The definition of highly erodible land and tolerable soil loss. Journal of Soil and Water Conservation 43:35-38.

Bledsoe, B. P. 2002. Stream erosion potential and stormwater management strategies. Journal of Water Resources Planning and Management 128:451-455.

Bódis, E., B. Tóth, & R. Sousa. 2014. Massive mortality of invasive bivalves as a potential resource subsidy for the adjacent terrestrial food web. Hydrobiologia 735: 253-262.

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

Bonar, S. A., W. A. Hubert, and D. W. Willis. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.

Bovee, K. D. & T. Cochnauer. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fisheries. Instream Flow Information Paper, US Fish and Wildlife Service: 53 p.

Box, J. B. and J. Mossa. 1999. Sediment, land use, and freshwater mussels: prospects and problems. Journal of the North American Benthological Society 18:99-117.

Brewer, S. K., C. F. Rabeni, S. P. Sowa, and G. Annis. 2007. Natural landscape and stream segment attributes influencing the distribution and relative abundance of riverine smallmouth bass in Missouri. North American Journal of Fisheries Management 27:326-341.

Brown, K. M., G. George, and W. Daniel. 2010. Urbanization and a threatened freshwater mussel: evidence from landscape scale studies. Hydrobiologia 655:189-196.

Buchanan, A. C. 1980. Mussels (naiades) of the Meramec River basin, Missouri. Missouri Department of Conservation, Jefferson City, MO: 76 p.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, 514 p.

Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference understanding AIC and BIC in model selection. Sociological Methods & Research 33:261-304.

Christian, A. D. and J. L. Harris. 2005. Development and assessment of a sampling design for mussel assemblages in large streams. The American Midland Naturalist 153:284-292.

Collier, J. S. & C. J. Brown. 2005. Correlation of sidescan backscatter with grain size distribution of surficial seabed sediments. Marine Geology 214: 431-449.

Colombet, I., M. C. Jaulent, P. Degoulet, & G. Chatellier. 2001. Logistic regression model: an assessment of variability of predictions. Studies in Health Technology and Informatics 84: 1314-1318.

Combes, M. and D. Edds. 2005. Mussel Assemblages Upstream from Three Kansas Reservoirs. Journal of Freshwater Ecology 20:139-148.

Cope, W. G. and D. L. Waller. 1995. Evaluation of fresh-water mussel relocation as a conservation and management strategy. Regulated Rivers Research & Management 11:147-155.

Cucherousset, J., J.-M. Roussel, R. Keeler, R. A. Cunjak, and R. Stump. 2005. The Use of Two New Portable 12-mm PIT Tag Detectors to Track Small Fish in Shallow Streams. North American Journal of Fisheries Management 25:270-274.

Cummings, K. S. and C. A. Mayer. 1992. Field guide to freshwater mussels of the Midwest. Illinois Natural History Survey Champaign, Illinois, 208 p.

Cyr, H., D. M. L. Storisteanu, and M. S. Ridgway. 2012. Sediment accumulation predicts the distribution of a unionid mussel (*Elliptio complanata*) in nearshore areas of a Canadian Shield lake. Freshwater Biology 57:2125-2140.

Daniel, W. M. and K. M. Brown. 2013. Multifactorial model of habitat, host fish, and landscape effects on Louisiana freshwater mussels. Freshwater Science 32:193-203.

Daraio, J. A., J. D. Bales, and T. J. Pandolfo. 2014. Effects of land use and climate change on stream temperature II: threshold exceedance duration projections for freshwater mussels. Journal of the American Water Resources Association 50:1177-1190.

Daraio, J. A., L. J. Weber, and T. J. Newton. 2010. Hydrodynamic modeling of juvenile mussel dispersal in a large river: the potential effects of bed shear stress and other parameters. Journal of the North American Benthological Society 29:838-851.

Dartnell, P. and J. V. Gardner. 2004. Predicting seafloor facies from multibeam bathymetry and backscatter data. Photogrammetric Engineering and Remote Sensing 70: 1081-1091.

Davis, E. A., A. T. David, K. M. Norgaard, T. H. Parker, K. McKay, C. Tennant, T. Soto, K. Rowe, and R. Reed. 2013. Distribution and abundance of freshwater mussels in the mid Klamath subbasin, California. Northwest Science 87:189-206.

Degraer, S., V. Van Lancker, G. Moerkerke, G. Van Hoey, K. Vanstaen, M. Vincx, and J. P. Henriet. 2003. Evaluation of the ecological value of the foreshore: habitat-model and macrobenthic sidescan sonar interpretation: extension along the Belgian Coastal Zone. Final report. Ministry of the Flemish Community, Environment and Infrastructure. Department. Waterways and Marine Affairs Administration, Coastal Waterways.

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

Dodds, W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. BioScience 54:205-216.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, and P. J. Leitão. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:027-046.

Downing, J. A., P. V. Meter, and D. A. Woolnough. 2010. Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels. Animal Biodiversity and Conservation 33:151-185.

Edsall, T. A., G. W. Kennedy, & W. H. Horns. 1993. Distribution, abundance, and resting microhabitat of burbot on Julian's Reef, southwestern Lake Michigan. Transactions of the American Fisheries Society 122: 560-574.

Field, A. & J. Miles. 2010. Discovering Statistics Using SAS. SAGE Publications.

Fish, J. P. & H. A. Carr. 1990. Sound underwater images: A guide to the generation and interpretation of side scan sonar data. Lower Cape Pub.

Fish, J. P. & H. A. Carr. 2001. Sound reflections: advanced applications of side scan sonar. Lower Cape Pub.

Fisher, B. E. 2013. Current status of freshwater mussels (Order Unionoida) in the Wabash River drainage of Indiana. Pages 103-109 in Proceedings of the Indiana Academy of Science.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data 365:2187-2200.

French, S. K. and J. D. Ackerman. 2014. Responses of newly settled juvenile mussels to bed shear stress: implications for dispersal. Freshwater Science 33:46-55.

Galbraith, H. S. and C. C. Vaughn. 2009. Temperature and food interact to influence gamete development in freshwater mussels. Hydrobiologia 636:35-47.

Galbraith, H. S., D. E. Spooner, and C. C. Vaughn. 2010. Synergistic effects of regional climate patterns and local water management on freshwater mussel communities. Biological Conservation 143:1175-1183.

Gangloff, M. and J. Feminella. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, USA. Freshwater Biology 52:64-74.

Ganser, A. M. 2012. The effects of elevated water temperatures on adult and juvenile freshwater mussels. College of Science, Masters Thesis, 72 p.

Girvetz, E. H., C. Zganjar, G. T. Raber, E. P. Maurer, P. Kareiva, and J. J. Lawler. 2009. Applied climate-change analysis: the Climate Wizard tool. Plos One 4:e8320.

Golladay, S. W., P. Gagnon, M. Kearns, J. M. Battle, and D. W. Hicks. 2009. Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. Journal of the North American Benthological Society 23:494-506.

Gordon, N. D. 2004. Stream hydrology: An introduction for ecologists. Wiley, West Sussex, England, 448 p.

Gough, H. M., A. M. G. Landis, and J. A. Stoeckel. 2012. Behaviour and physiology are linked in the responses of freshwater mussels to drought. Freshwater Biology 57:2356-2366.

Graf, D. L. & D. O ´. Foighil. 2000. The evolution of brooding characters among the freshwater pearly mussels (Bivalvia:Unionoidea) of North America. Journal of Molluscan Studies 66: 157–170.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84: 2809-2815.

Haag, W. R. 2012. North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, Cambridge, UK, 538 p.

Haag, W. R. and J. D. Williams. 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735:45-60.

Hale, J. R., J. V. Bouma, B. Vadopalas, and C. S. Friedman. 2012. Evaluation of Passive Integrated Transponders for Abalone: Tag Placement, Retention, and Effect on Survival. Journal of Shellfish Research 31:789-794.

Haltuch, M. A., P. A. Berkman, & D. W. Garton. 2000. Geographic information system (GIS) analysis of ecosystem invasion: Exotic mussels in Lake Erie. Limnology and Oceanography 45: 1778-1787.

Hardison, B. S. and J. B. Layzer. 2001. Relations between complex hydraulics and the localized distribution of mussels in three regulated rivers. Regulated Rivers: Research & Management 17:77-84.

Hartstein, N. D. 2005. Acoustical and sedimentological characterization of substrates in and around sheltered and open-ocean mussel aquaculture sites and its bearing on the dispersal of mussel debris. Ieee Journal of Oceanic Engineering 30: 85-94.

Hastie, L. C. & P. J. Cosgrove. 2002. Intensive searching for mussels in a fast-flowing river: An estimation of sampling bias. Journal of Conchology 37: 309-316.

Henley, W., M. Patterson, R. Neves, and A. D. Lemly. 2000. Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. Reviews in Fisheries Science 8:125-139.

Hewitt, J. E., S. E. Thrush, P. Legendre, G. A. Funnell, J. Ellis, & M. Morrison. 2004. Mapping of marine soft-sediment communities: Integrated sampling for ecological interpretation. Ecological Applications 14: 1203-1216.

Hilbe, J. M. 2011. Negative binomial regression. Cambridge University Press.

Hincks, S. S. and G. L. Mackie. 1997. Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth, and reproductive success of zebra mussel (Dreissena

polymorpha) in Ontario lakes. Canadian Journal of Fisheries and Aquatic Sciences 54:2049-2057.

Hobbs, C. H. 1985. Sidescan sonar as a tool for mapping spatial variations in sediment type. Geo-Marine Letters 5: 241-245.

Hoftyzer, E., J. D. Ackerman, T. J. Morris, and G. L. Mackie. 2008. Genetic and environmental implications of reintroducing laboratory-raised unionid mussels to the wild. Canadian Journal of Fisheries and Aquatic Sciences 65:1217-1229.

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.

Hook, J. D. 2011. Sturgeon habitat quantified by sidescan sonar imagery. University of Georgia.

Hopkins II, R. L. 2009. Use of landscape pattern metrics and multiscale data in aquatic species distribution models: a case study of a freshwater mussel. Landscape Ecology 24:943-955.

Hornbach, D. J., V. J. Kurth, and M. C. Hove. 2010. Variation in freshwater mussel shell sculpture and shape along a river gradient. The American Midland Naturalist 164:22-36.

Howard, J. K. and K. M. Cuffey. 2003. Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls. Journal of the North American Benthological Society 22:63-77.

Howard, J. K. and K. M. Cuffey. 2006. The functional role of native freshwater mussels in the fluvial benthic environment. Freshwater Biology 51:460-474.

Isom, B. G. and C. Gooch. 1986. Rationale for Sampling and Interpretation of Ecological Data in the Assessment of Freshwater Ecosystems. ASTM Special Technical Pub No. 894.

Jones, J. W. and R. J. Neves. 2011. Influence of life-history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 21: 57-73.

Kaeser, A. J. and T. L. Litts. 2008. An assessment of deadhead logs and large woody debris using side scan sonar and field surveys in streams of southwest Georgia. Fisheries 33: 589-597.

Kaeser, A. J. and T. L. Litts. 2010. A novel technique for mapping habitat in navigable streams using low-cost side scan sonar. Fisheries 35: 163-174.

Kaeser, A. J., T. L. Litts, and T. Tracy. 2012. Using low-cost sidescan sonar for benthic mapping throughout the Lower Flint River, Georgia, USA. River Research and Applications.

Kaufmann, P. R., U. S. E. P. A. E. Monitoring, and A. Program. 1999. Quantifying physical habitat in wadeable streams. Environmental Monitoring and Assessment Program, National Health and Environmental Effects Research Laboratory, Office of Research and Development, US Environmental Protection Agency.

Kurth, J., C. Loftin, J. Zydlewski, and J. Rhymer. 2007. PIT tags increase effectiveness of freshwater mussel recaptures. Journal of the North American Benthological Society 26:253-260.

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

LeBlanc, R. T., R. D. Brown, and J. E. FitzGibbon. 1997. Modeling the effects of land use change on the water temperature in unregulated urban streams. Journal of Environmental Management 49:445-469.

Lopes-Lima, M., A. Teixeira, E. Froufe, A. Lopes, S. Varandas, & R. Sousa. 2014. Biology and conservation of freshwater bivalves: past, present and future perspectives. Hydrobiologia 735: 1-13.

March, F. A., F. J. Dwyer, T. Augspurger, C. G. Ingersoll, N. Wang, and C. A. Mebane. 2007. An evaluation of freshwater mussel toxicity data in the derivation of water quality guidance and standards for copper. Environmental Toxicology and Chemistry 26:2066-2074.

Marchetti, M. P., T. Light, P. B. Moyle, and J. H. Viers. 2004. Fish invasions in California watersheds: Testing hypotheses using landscape patterns. Ecological Applications 14:1507-1525.

Master, L. L., B. A. Stein, L. S. Kutner, and G. A. Hammerson. 2000. Vanishing assets: conservation status of US species. In Stein, B. A., L. S., Kutner, & J. S. Adams (eds), Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, England: 93-118.

Mazerolle, M. J. 2004. Appendix 1: Making sense out of Akaike's Information Criterion (AIC): its use and interpretation in model selection and inference from ecological data. Mouvements et Reproduction des Amphibiens en Tourbières Perturbées:174-190.

McRae, S., J. D Allan, and J. Burch. 2004. Reach-and catchment-scale determinants of the distribution of freshwater mussels (Bivalvia: Unionidae) in south-eastern Michigan, USA. Freshwater Biology 49:127-142.

Metcalfe-Smith, J. L., J. Di Maio, S. K. Staton, and G. L. Mackie. 2000. Effect of sampling effort on the efficiency of the timed search method for sampling freshwater mussel communities. Journal of the North American Benthological Society 19:725-732.

Meybeck, M. 1987. Global chemical weathering of surficial rocks estimated from river dissolved loads. American Journal of Science 287:401-428.

Milam, C., J. Farris, F. Dwyer, and D. Hardesty. 2005. Acute toxicity of six freshwater mussel species (glochidia) to six chemicals: Implications for daphnids and *Utterbackia imbecillis* as surrogates for protection of freshwater mussels (Unionidae). Archives of Environmental Contamination and Toxicology 48:166-173.

Miller, A. C. & B. S. Payne. 1993. Qualitative versus quantitative sampling to evaluate population and community characteristics at a large-river mussel bed. American Midland Naturalist 130: 133-145.

Miller, A. C. and B. S. Payne. 2001. An investigation of mussel resources in selected bayous, northerwestern Mississippi, 1999 and 2000. DTIC Document.

Miller, R. B., G. A. Fox, C. J. Penn, S. Wilson, A. Parnell, R. A. Purvis, and K. Criswell. 2014. Estimating sediment and phosphorus loads from streambanks with and without riparian protection. Agriculture, Ecosystems & Environment 189:70-81.

Morales, Y., L. Weber, A. Mynett, and T. Newton. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. Journal of the North American Benthological Society 25:664-676.

Morell, V. 2008. Into the wild: reintroduced animals face daunting odds. Science 320:742-743.

Naimo, T. J. 1995. A review of the effects of heavy metals on freshwater mussels. Ecotoxicology 4: 341-362.

Nakato, T., J. Christensen, and B. Schonhoff. 2007. Freshwater mussel survey in pool 16, the Mississippi River, near Fairport, Iowa: Rm 463.5—rm 464.1, approximately. IIHR technical report 464, The University of Iowa, IIHR—Hydroscience & Engineering.

National Native Mussel Conservation Committee. 1998. National strategy for the conservation of native freshwater mussels. Journal of Shellfish Research 17: 1419-1428.

Neves, R. J. 1993. A state-of-the-unionids address. Proceedings of the UMRCC Symposium on the Conservation and Management of Freshwater Mussels.

Newton, R. and A. Stefanon. 1975. Application of sidescan sonar in marine biology. Marine Biology 31: 287-291.

Newton, T. J., D. A. Woolnough, and D. L. Strayer. 2008. Using landscape ecology to understand and manage freshwater mussel populations. Journal of the North American Benthological Society 27:424-439.

Onda, Y., Y. Komatsu, M. Tsujimura, and J. i. Fujihara. 2001. The role of subsurface runoff through bedrock on storm flow generation. Hydrological Processes 15:1693-1706.

Osterling, M. E., B. L. Arvidsson, and L. A. Greenberg. 2010. Habitat degradation and the decline of the threatened mussel Margaritifera margaritifera: influence of turbidity and sedimentation on the mussel and its host. Journal of Applied Ecology 47:759-768.

Peck, A., J. L. Harris, J. L. Farris, and A. D. Christian. 2007. Assessment of freshwater mussel relocation as a conservation strategy.

Peterson, J. T. and C. F. Rabeni. 2001. Evaluating the physical characteristics of channel units in an Ozark stream. Transactions of the American Fisheries Society 130:898-910.

Piégay, H., S. Darby, E. Mosselman, and N. Surian. 2005. A review of techniques available for delimiting the erodible river corridor: a sustainable approach to managing bank erosion. River Research and Applications 21:773-789.

Pigg, J. 1977. A survey of the fishes of the Muddy Boggy River in south central Oklahoma. Oklahoma Academy of Science 57:68-82.

Poole, K. E. and J. A. Downing. 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. Journal of the North American Benthological Society 23:114-125.

Pusey, B. J. and A. H. Arthington. 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. Marine and Freshwater Research 54:1-16.

Rempel, L. L., J. S. Richardson, and M. C. Healey. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. Freshwater Biology 45:57-73.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53:295-311.

Riley, W. D., M. O. Eagle, M. J. Ives, P. Rycroft, and A. Wilkinson. 2003. A portable passive integrated transponder multi-point decoder system for monitoring habitat use and behaviour of freshwater fish in small streams. Fisheries Management and Ecology 10:265-268.

Rosgen, D. L. 1994. A classification of natural rivers. Catena 22:169-199.

Schwalb, A. N., K. Cottenie, M. S. Poos, and J. D. Ackerman. 2011. Dispersal limitation of unionid mussels and implications for their conservation. Freshwater Biology 56:1509-1518.

Schwalb, A. N., T. J. Morris, N. E. Mandrak, and K. Cottenie. 2013. Distribution of unionid freshwater mussels depends on the distribution of host fishes on a regional scale. Diversity and Distributions 19:446-454.

Schwendel, A. C., R. G. Death, and I. C. Fuller. 2010. The assessment of shear stress and bed stability in stream ecology. Freshwater Biology 55:261-281.

Shea, C. P., J. T. Peterson, M. J. Conroy, and J. M. Wisniewski. 2013. Evaluating the influence of land use, drought and reach isolation on the occurrence of freshwater mussel species in the lower Flint River Basin, Georgia (USA). Freshwater Biology 58:382-395.

Smith, A. C., N. Koper, C. M. Francis, and L. Fahrig. 2009. Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. Landscape Ecology 24:1271-1285.

Smith, D. R., R. F. Villella, & D. P. Lemarie. 2003. Application of adaptive cluster sampling to low-density populations of freshwater mussels. Environmental and Ecological Statistics 10: 7-15.

Smith, D. R., R. F. Villella, and D. P. Lemarié. 2001. Survey protocol for assessment of endangered freshwater mussels in the Allegheny River, Pennsylvania. Journal of the North American Benthological Society 20:118-132.

Smith, J. R., P. Fong, and R. F. Ambrose. 2006. Dramatic declines in mussel bed community diversity: response to climate change? Ecology 87:1153-1161.

Smith, T. A. and E. S. Meyer. 2010. Freshwater mussel (Bivalvia: Unionidae) distributions and habitat relationships in the navigational pools of the Allegheny River, Pennsylvania. Northeastern Naturalist 17:541-564.

Sousa, R., S. Varandas, R. Cortes, A. Teixeira, M. Lopes-Lima, J. Machado, & L. Guilhermino. 2012. Massive die-offs of freshwater bivalves as resource pulses. Annales de Limnologie 48: 105-112.

Spooner, D. E. and C. C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. Oecologia 158:307-317.

Steuer, J. J., T. J. Newton, and S. J. Zigler. 2008. Use of complex hydraulic variables to predict the distribution and density of unionids in a side channel of the Upper Mississippi River. Hydrobiologia 610:67-82.

Stevenson, R. J. 1997. Scale-dependent determinants and consequences of benthic algal heterogeneity. Journal of the North American Benthological Society 16:248-262.

Strayer, D. L. 1981. Notes on the microhabitats of unionid mussels in some Michigan streams. American Midland Naturalist 106:411-415.

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. 2008. Freshwater mussel ecology: A multifactor approach to distribution and abundance. University of California Press, Oakland, CA, 204 p.

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. 2006. The effects of surface geology and stream size on freshwater mussel (Bivalvia, Unionidae) distribution in southeastern Michigan, USA. Freshwater Biology 13:253-264.

Strayer, D. L. and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29:344-358.

Strayer, D. L. and D. R. Smith. 2003. A guide to sampling freshwater mussel populations. American Fisheries Society Monograph 8, Bethesda, MD. 110 p.

Strayer, D. L. and J. Ralley. 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., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves - A case study of zebra mussels in the Hudson River. BioScience 49:19-27.

Sullivan, K. P. and C. M. Gale. 1999. A comparison of channel catfish catch rates, size distributions, and mortalities using three different gears in a Missouri impoundment. Pages 293-300 in Catfish 2000: proceedings of the international ictalurid symposium. American Fisheries Society, Symposium.

Sweeney, B. W., T. L. Bott, J. K. Jackson, L. A. Kaplan, J. D. Newbold, L. J. Standley, W. C. Hession, and R. J. Horwitz. 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proceedings of the National Academy of Sciences of the United States of America 101:14132-14137.

Teixeira, J. B., A. S. Martins, H. T. Pinheiro, N. A. Secchin, R. L. de Moura, & A. C. Bastos. 2013. Traditional ecological knowledge and the mapping of benthic marine habitats. Journal of Environmental Management 115: 241-250.

Ten Brinke, W., P. G. Augustinus, and G. W. Berger. 1995. Fine-grained sediment deposition on mussel beds in the Oosterschelde (The Netherlands), determined from echosoundings, radio-isotopes and biodeposition field experiments. Estuarine, Coastal and Shelf Science 40:195-217.

Theuerkauf, J., S. Rouys, and C. Chatreau. 2007. Mortality of radio-tracked wild rats in relation to transmitter weight and resilience of transmitters in relation to their design Journal of the Royal Society of New Zealand 37:85-90.

Theler, J. 1987. Prehistoric freshwater mussel assemblages of the Mississippi River in southwestern Wisconsin. The Nautilus 101:143-150.

Thomas, G. R., J. Taylor, and C. G. d. Leaniz. 2010. Captive breeding of the endangered freshwater pearl mussel *Margaritifera margaritifera*. Endangered Species Research 12:1-9.

Tiemann, J. S., K. S. Cummings, and C. A. Phillips. 2011a. Mollusks of the Shawnee National Forest, Illinois. Illinois Natural History Survey.

Tiemann, J. S., S. E. McMurray, M. C. Barnhart, and G. T. Watters. 2011b. A review of the interactions between catfishes and freshwater mollusks in North America. Pages 733-743 in American Fisheries Society Symposium, Bethesda.

Toweill, D. E. 1974. Winter food habits of river otters in western Oregon. The Journal of Wildlife Management 38:107-111.

Tyrrell, M. and D. J. Hornbach. 1998. Selective predation by muskrats on freshwater mussels in two Minnesota rivers. Journal of the North American Benthological Society 17:301-310.

Van Der Schalie, H. and A. Van Der Schalie. 1950. The mussels of the Mississippi River. American Midland Naturalist 44:448-466.

Vanleeuwen, D. J. and J. A. Arruda. 2001. A survey of the unionid mussels in six tributaries of the lower Neosho River (Kansas). Transactions of the Kansas Academy of Science 104:164-177.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Vaughn, C. C. and C. C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biology 46:1431-1446.

Vaughn, C. C. and C. M. Taylor. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conservation Biology 13:912-920.

Vaughn, C. C. and C. M. Taylor. 2000. Macroecology of a host-parasite relationship. Ecography 23:11-20.

Vaughn, C. C., K. B. Gido, and D. E. Spooner. 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance. Hydrobiologia 527:35-47.

Vaughn, C. C., S. J. Nichols, and D. E. Spooner. 2008. Community and foodweb ecology of freshwater mussels. Journal of the North American Benthological Society 27:409-423.

Vaughn, C., C. M. Taylor, and K. J. Eberhard. 1995. A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys. Pages 157-162 In: Cummings, K.S., A.C. Buchanan, C.A. Mayer, and T.J. Naimo (eds.) Conservation and management of freshwater mussels II: initiatives for the future. Proceedings of a UMRCC Symposium, 16-18 October 1995, St. Louis, MO. Upper Mississippi River Conservation Committee, Rock Island, IL.

Waters, T. F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7. Bethesda, MD. 270 p.

Watters, G. T. 1994a. An annotated bibliography of the reproduction and propagation of the Unionoidea:(primarily of North America). Ohio Biological Survey, College of Biological Sciences, The Ohio State University, Columbus, OH. 164 p.Watters, G. T. 1994b. Form and function of unionoidean shell sculpture and shape (Bivalvia). American Malacological Bulletin 11:1-20.

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. Pages 261-274 in Proceedings of the First Freshwater Mollusk Conservation Society Symposium.

Wenger, S. 1999. A review of the scientific literature on riparian buffer width, extent and vegetation. Available at http://www.utexas.edu/law/centers/cppdr/services/Improving%20Streams%20web/Work%20Groups/Public%20Lands/Wegner_1999_Review_of_buffer_width.pdf, Accessed December 13, 2014.

Widdows, J., J. S. Lucas, M. D. Brinsley, P. N. Salkeld, and F. J. Staff. 2002. Investigation of the effects of current velocity on mussel feeding and mussel bed stability using an annular flume. Helgoland Marine Research 56:3-12.

Williams, J. D., M. L. Warren Jr, K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18:6-22.

Wilson, C. D., D. Roberts, and N. Reid. 2011. Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.). Biological Conservation 144:821-829.

Wilson, C. D., G. Arnott, and D. Roberts. 2011. The pitfall with PIT tags: marking freshwater bivalves for translocation induces short-term behavioural costs. Animal Behaviour 81:341-346.

Woods A. J., J. M. Omernik, D. R. Butler et al. 2005. Ecoregions of Oklahoma (color poster with map, descriptive text, summary tables, and photographs). U.S. Geological Survey, Reston, Virginia. Available at: http://www.epa.gov/wed/pages/ecoregions/ok_eco.htm.

Young, S. P. and J. J. Isely. 2008. Evaluation of methods for attaching PIT tags and biotelemetry devices to freshwater mussels. Molluscan Research 28:175-178.

Zigler, S. J., T. J. Newton, M. Davis, and J. T. Rogala. 2012. Patterns in species richness and assemblage structure of native mussels in the Upper Mississippi River. Aquatic Conservation: Marine and Freshwater Ecosystems 22:577-587.

Zipper, C. E., B. Beaty, G. C. Johnson, J. W. Jones, J. L. Krstolic, B. J. Ostby, W. J. Wolfe, and P. Donovan. 2014. Freshwater mussel population status and habitat quality in the Clinch River, Virginia and Tennessee, USA: a featured collection. Journal of the American Water Resources Association 50:807-819.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, 596 p.

Table 1- Descriptive statistics (mean and range) of environmental variables used for landscape modeling. Land use= percent of agriculture and pasture lands.

Variable	Abbreviation	Muddy Boggy	Clear Boggy
Width-to-depth ratio	WD	29.79 (19.60-51.38)	24.57 (11.40-51.18)
Highly erodible land	HEL	48% (43%-54%)	40% (34%-48%)
Shale	Geo	46% (4%-85%)	37% (6%-70%)
Riparian corridor width (1 m^2)	Rip	138.95 (76.00-196.20)	113.67 (43.40-206.40)
Land use	Land	21% (0%-47%)	27% (0%-73%)
Forest cover	Forest	69% (45%-88%)	63% (27%-88%)
Sinuosity	Sin	1.38 (1.02-1.87)	1.56 (1.13-2.37)
Drainage area (1 km^2)	Drain	2193.30 (119.61-5860.83)	1443.64 (303.94-2588.89)

Table 2- Environmental variables and associated spatial scales related to distributions of freshwater mussels. Spatial scale: catchment (drainage area), segmentshed (tributary to tributary), buffer (200 m wide and 1 km upstream of study site), reach (40 times wetted width), and microhabitat (<1 m).

	Spatial Scale				
Environmental Variables	Catchment	Segmentshed	Buffer	Reach	Microhabitat
Stream size	X	X			
Geology	X	X			
Forest cover			X	X	
Land use	X	X	X		
Soil	X	X			
Riparian corridor			X	X	
Sinuosity		X			
Bank soil composition				X	
W:D ratio				X	
Substrate composition					X

Table 3- Sources and resolution of geospatial data used in landscape model analyses.

Variable	Source	Resolution
Stream size	http://dategateway.nrcs.gov/NHDPlusV2	1:100,000 scale
Geology	http://datagateway.nrcs.usda.gov	1:100,000 scale (vector)
Soil (HEL)	http:// www.soildatamart.nrcs.usda.gov	lat: 0.0000001 long: 0.0000001 (vector)
Land use	http://datagateway.nrcs.usda.gov	1 m
Riparian corridor	http://datagateway.nrcs.usda.gov/NAIP	1 m
Forest cover	http://datagateway.nrcs.usda.gov	1 m

Table 4- Hypotheses developed to predict mussel presence for AIC model ranking. Positive relationship indicated by "+" and negative relationship indicate by "–". Variables are: HEL= proportion of highly erodible land, Geology= proportion of shale, Land use= proportion of agriculture/pasture land, Forest cover= proportion of forested vegetation.

Species	Hypotheses	Rationale	Reference
Bleufer	1: Presence is – related HEL and + related to riparian corridor width	Fine sediment can impair respiratory function, riparian corridor can buffer against fine sediment	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004)
	2: Presence is + related to drainage area and W:D ratios	Typically found in the downstream portions of large rivers	Cummings and Mayer (1992), Vanleeuwen and Arruda (2001)
	3: Presence is + related to drainage area and – related to HEL	Influence timing and input of fine sediments	McRae et al. (2004), Strayer (2006)
	4: Presence is – related to geology, land use, and + related to W:D ratios	Water quality important to development and adequate respiratory function	Box and Mossa (1999), Arbuckle and Downing (2002)
Fragile papershell	1: Presence is – related HEL and + related to riparian corridor width	Typically found in the downstream portions of rivers and related to the mainstem	Vanleeuween and Arruda (2001)
	2: Presence is + related to riparian corridor width, – related to HEL, and bank erodibility	Fine sediment can impair respiratory function, riparian corridor can buffer against fine sediment	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004)
	3: Presence is + related to drainage area, W:D ratios, and – related to HEL	Influence timing and input of fine sediments	McRae et al. (2004), Strayer (2006)
	4: Presence is + related to drainage area, sinuosity, and – related to HEL	Influence timing and input of fine sediments	McRae et al. (2004), Strayer (2006)

Pimpleback	1: Presence is + related to drainage area	Typically found in the downstream portions of rivers	Vanleeuween and Arruda (2001), Fisher (2013)
	2: Presence is – related to geology and + related to forest cover	Water quality important to development and adequate respiratory function	McRae et al. (2004), Strayer (2006)
	3: Presence is + related to drainage area, – related to HEL and bank erodibility	Influence timing and input of fine sediments, fine sediment can impair respiratory function	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004)
	4: Presence is + related to drainage area, – related to geology, and + related to W:D ratios	Influence hydrology and water quality, effecting respiratory and stability	Vanleeuween and Arruda (2001), Strayer (2006)
Wabash pigtoe	1: Presence is + related to land use	Tolerant of limited amounts of fine sediments and increased pollution	Theler (1987), Cummings and Mayer (1992)
	2: Presence is – related to drainage area and riparian corridor width	Influence timing and input of fine sediments, riparian corridor can buffer against fine sediment	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004)
	3: Presence is – related to riparian corridor width and bank erodibility	Fine sediment can impair respiratory function, riparian corridor can buffer against fine sediment	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004)
	4: Presence is – related to HEL,+ related to land use, and – related to bank erodibility	Tolerant of limited amounts of fine sediments and increased pollution	Theler (1987), Cummings and Mayer (1992)

Table 5- Hypotheses developed to predict mussel densities for AIC model ranking. Positive relationship indicated by "+" and negative relationship indicate by "–". Variables are: W:D= width-to-depth ratio, Geology= proportion of shale, Land use= proportion of agriculture/pasture land, Forest cover= proportion of forested vegetation.

Species	Hypothesis	Rationale	Reference
Bleufer	1: Density is + related to drainage area and riparian corridor width	Fine sediment can impair respiratory function, riparian corridor can buffer against fine sediment	Wenger (1999), Sweeney et al. (2004), Strayer (2006)
	2: Density is + related to drainage area and W:D ratios	Typically occurs at higher densities in downstream portions of large rivers	Cummings and Mayer (1992), Vanleeuwen and Arruda (2001), Strayer (2006)
	3: Density is – relayed to geology and + related to substrate	Influence hydrology, slope, and turbidity which effect habitat and species numbers	Arbuckle and Downing (2002), Strayer (2006)
	4: Density is + related to drainage area, sinuosity, and – related to geology	Influences stream power and bed-load transport reducing suitable habitat	Box and Mossa (1999), Arbuckle and Downing (2002), Strayer (2006)
Fragile papershell	1: Density is + related to drainage area and – related to geology	Influences stream power and bed-load transport reducing suitable habitat	Box and Mossa (1999), Arbuckle and Downing (2002), Strayer (2006)
	2: Density is – related to geology and + related to W:D	Influence hydrology, slope, and turbidity which effect habitat and species numbers	Arbuckle and Downing (2002), Strayer (2006)
	3: Density is + related to drainage area and W:D ratios	Typically occurs at higher densities in downstream portions of large rivers	Cummings and Mayer (1992), Vanleeuwen and Arruda (2001), Strayer (2006)

	4: Density + related to drainage area, W:D, and – related to geology	Influences stream power and bed-load transport reducing suitable habitat	Box and Mossa (1999), Arbuckle and Downing (2002), Strayer (2006)
Pimpleback	1: Density is + related to drainage area	Typically found in the downstream portions of rivers	Vanleeuween and Arruda (2001), Fisher (2013)
	2: Density is + related to drainage area and – related to geology	Influences stream power and bed-load transport reducing suitable habitat	Box and Mossa (1999), Arbuckle and Downing (2002), Strayer (2006)
	3: Density is – related to geology and + related to forest cover	Water quality and fine sediment inputs effect species numbers	McRae et al. (2004), Sweeney et al. (2004), Strayer (2006)
	4: Density is + related to drainage area, forest cover, and substrate	Influence habitat availability, fine sediments, and stability	Vanleeuween and Arruda (2001), Sweeney et al. (2004), Strayer (2006)
Wabash pigtoe	1: Density is + related to land use	Tolerant of limited amounts of fine sediments and increased phosphorus	Theler (1987), Cummings and Mayer (1992)
	2: Density is + related to W:D and – related to riparian corridor width	Influence bedload transport and deposit of suspended sediments	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004)
	3: Density is – related to riparian corridor width, forest cover, W:D, and substrate	Bedload transport and fine sediment inputs effect species numbers	Cummings and Mayer (1992), Box and Mossa (1999), Sweeney et al. (2004)

Table 6- Hypotheses developed to predict mussel-bed presence for AIC model ranking. Positive relationship indicated by "+" and negative relationship indicated by "–".Variables are: HEL= proportion of highly erodible land, Geology= proportion of shale, Land use= proportion of agriculture/pasture land.

Hypothesis	Rationale	Reference
1: Presence is + related to drainage area, and – related to land use	Influence quality habitat, and timing and input of fine sediments, can effect respiratory function	Strayer (1993), Box and Mossa (1999), McRae et al. (2004)
2: Presence is + related drainage area, – related to geology, and + related to sinuosity	Influence hydrology and water quality, important to development and proper respiratory function	Strayer (1993), Box and Mossa (1999), McRae et al. (2004), Strayer (2006), Atkinson et al. (2012)
3: Presence is + related riparian corridor width, – related to bank erodibility, and HEL	Fine sediment can impair respiratory function, riparian corridor can buffer against fine sediment	Box and Mossa (1999), Wenger (1999), Sweeney et al. (2004), Strayer (2006)
4: Presence is + related drainage area, – related to HEL, and land use	Influence quality habitat, and timing and input of fine sediments, can effect respiratory functions	Strayer (1993), Box and Mossa (1999), McRae et al. (2004)

Table 7- Matrix of *r*-values for Spearman's rank correlation coefficient of mussel bed habitat variables. Values of 0.30 or more are considered multicollinear for multiple regression scenarios and are indicated by asterisks. Variables are: BFD= bankfull depth, BFW= bankfull width, W:D= width to depth ratio, and SS= shear stress.

	Depth	BFD	BFW	Sinuosity	W:D	SS
Substrate	-0.10	-0.02	-0.32*	0.65*	-0.06	-0.02
Depth		0.26	0.21	-0.04	-0.10	0.26
BFD			0.01	0.53*	-0.84*	1.00*
BFW				-0.33*	0.44*	0.01
Sinuosity					-0.49*	0.53*
W:D						-0.84*

Table 8- Model output values of beta, standard error, odds ratio and confidence intervals for a model relating habitat conditions with the presence of mussel beds as observed by sidescan sonar samples.

			95% CI for Odds Ratio		
	B	SE	Lower	Odds Ratio	Upper
Intercept	14.89	10.14			
Depth	-5.97	3.52	<0.001	0.003	2.54
W:D	-0.08	0.28	0.53	0.92	1.61
Sinuosity	-0.69	1.55	0.02	0.50	10.47

Table 9- Total number of individual mussel species systematically sampled during 2012 and 2013. Site codes were described in Figure 2.

Species		Sampling Site										
		CB1	CB2	CB3	CB9	CB10	MB1	MB2	MB8	MB10	MB11	Total
Potamilis purpuratus	Bleufer	23	7	1	0	1	21	7	16	14	3	93
Truncilla truncata	Deertoe	1	2	16	1	0	3	8	0	5	4	40
Lampsilis siliquoidea	Fatmucket	0	0	0	0	1	0	0	0	1	0	2
Truncilla donaciformis	Fawnsfoot	0	2	1	0	0	2	9	0	4	1	19
Leptodea fragilis	Fragile Papershell	13	5	7	0	2	29	36	3	17	1	113
Quadrula quadrula	Mapleleaf	3	0	9	0	3	7	4	6	4	21	57
Utterbackia imbecillis	Paper Pondshell	0	0	0	0	0	0	0	0	2	0	2
Quadrula pustulosa	Pimpleback	24	19	19	12	13	4	49	0	9	4	153
Potamilis ohiensis	Pink Papershell	0	0	0	0	0	1	1	0	1	0	3
Tritogonia verrucosa	Pistolgrip	3	19	9	16	10	4	42	6	33	6	148
Lampsilis cardium	Plain Pocketbook	5	3	8	1	1	1	3	0	2	0	24
Arcidens confragosus	Rock Pocketbook	0	0	1	0	0	0	1	0	1	0	3
Quadrula apiculata	Southern Mapleleaf	2	5	9	2	0	2	19	0	12	3	54
Obliquaria reflexa	Threehorn Wartyback	12	19	54	8	2	36	63	0	53	3	250

Amblema plicata	Threeridge	16	50	3	6	3	12	19	34	17	38	198
Fusconaia flava	Wabash pigtoe	11	19	4	158	136	0	13	28	28	21	418
Quadrula nodulata	Wartyback	18	18	31	6	4	14	30	4	10	11	146
Megalonaias nervosa	Washboard	3	15	17	1	1	4	26	17	54	26	164
Lasmingona complanata	White Heelsplitter	3	2	0	1	1	1	4	3	7	3	25
Lampsilis teres	Yellow Sandshell	9	6	4	3	5	10	1	11	11	10	70
Total		146	191	193	215	183	151	335	128	285	155	1982

Table 10- Minimum (min) and maximum (max) sizes of mussel species sampled using excavated quadrats in the Muddy Boggy (MB) and Clear Boggy (CB) rivers.

River	Species	n	Min height (mm)	Max height (mm)	Min length (mm)	Max length (mm)
MB	bluefer	61	47	110	69	184
	deertoe	19	17	60	28	79
	fatmucket	1	37	37	58	58
	fawnsfoot	16	12	26	19	42
	fragile papershell	85	13	75	24	127
	mapleleaf	42	8	74	10	92
	paper pondshell	2	63	70	109	114
	pimpleback	66	17	72	19	110
	pink papershell	3	48	64	73	99
	pistolgrip	90	7	85	8	139
	plain pocketbook	6	69	95	90	123
	rock pocketbook	2	69	70	100	105
	southern mapleleaf	36	22	71	23	89
	threehorn wartyback	154	20	60	28	80
	threeridge	118	31	127	37	220
	Wabash pigtoe	90	41	79	42	185
	wartyback	68	13	387	14	71
	washboard	127	19	144	23	234
	white heelsplitter	18	59	114	62	158
	yellow sandshell	42	27	59	55	114
CB	bluefer	32	10	88	16	141
	deertoe	20	31	48	38	59
	fatmucket	1	34	34	55	55
	fawnsfoot	3	8	13	13	22
	fragile papershell	27	7	75	12	110

mapleleaf	15	10	56	14	69
pimpleback	86	8	72	11	80
pistolgrip	56	33	75	32	122
plain pocketbook	18	49	86	69	113
rock pocketbook	1	63	63	92	92
southern mapleleaf	18	8	58	12	70
threehorn wartyback	95	25	71	33	96
threeridge	78	44	127	59	175
Wabash pigtoe	328	12	71	15	87
wartyback	76	11	60	13	71
washboard	37	10	127	13	195
white healsplitter	7	48	109	62	138
yellow sandshell	27	8	53	20	118

Table 11- Total number of individual fish species encountered during 2012 and 2013 fish sampling. Site codes are described in Figure 2.

Species	Common name	MB1	MB2	MB5	CB1	CB3	CB5	Total
Notropis boops	bigeye shiner			36		94		130
Ictiobus niger	black buffalo	1				1	1	3
Moxostoma duquesnei	black redhorse			1			6	7
Percina maculata	blackside darter	1						1
Cyprinella venusta	blacktail shiner	26		2		206	178	412
Cycleptus elongatus	blue sucker	6	8		6			20
Lepomis macrochirus	bluegill	22	3	85	40	34	27	211
Etheostoma chlorosomum	bluntnose darter				1			1
Pimephales notatus	bluntnose minnow	16		67	12	19	4	118
Labidesthes sicculus	brook silverside			34	2			36
Pimephales vigilax	bullhead minnow	17		5	11	25	7	65
Ictalurus punctatus	channel catfish	12	2	5	11	20	52	102
Percina copelandi	channel darter				1		1	2
Cyprinus carpio	common carp	1						1
Hybognathus hayi	cypress minnow					1		1
Percina sciera	dusky darter			3	3	5	5	16
Notropis atherinoides	emerald shiner			1		1		2
Pimephales promelas	fathead minnow	4				19		23
Pylodictis olivaris	flathead catfish		1		1		3	5
Noturus nocturnus	freckled madtom			2		3	3	8
Aplodinotus grunniens	freshwater drum	3			1			4
Dorosoma cepedianum	gizzard shad	1				1		2
Moxostoma erythrurum	golden redhorse			1				1
Notemigonus crysoleucas	golden shiner					3		3
Lepomis cyanellus	green sunfish			37	10	1	6	54
Micropterus salmoides	largemouth bass	2	1	4	6	1		14
Percina caprodes	logperch	1						1
Lepomis megalotis	longear sunfish	2	10	11	20	2	34	79
Lepisosteus osseus	longnose gar	11	1			13	4	29

Etheostoma asprigene	mud darter	1						1
Etheostoma radiosum	orangebelly darter	1						1
Lepomis humilis	orangespotted sunfish	129		47	26	23		225
Etheostoma spectabile	orangethroat darter			4			10	14
Notropis ozarcanus	ozark shiner				1			1
Opsopoeodus emiliae	pugnose minnow	4			1		1	6
Cyprinella lutrensis	red shiner	28			24	8		60
Lepomis microlophus	redear sunfish			11	10	14	15	50
Lythrurus umbratilis	redfin shiner	1		12	1		3	17
Carpiodes carpio	river carpsucker				1			1
Notropis rubellus	rossyface shiner				1	2		3
Notropis stramineus	sand shiner	91		20	27	3	6	147
Lepisosteus platostomus	shortnose gar	2			1			3
Percina phoxocephala	slenderhead darter				2	6	1	9
Etheostoma gracile	slough darter			2				2
Ictiobus bubalus	smallmouth buffalo	2	4		1	2	4	13
Micropterus punctulatus	spotted bass	1		1	4		5	11
Lepisosteus oculatus	spotted gar	2				1	4	7
Minytrema melanops	spotted sucker				1			1
Phenacobius mirabilis	suckermouth minnow					19	3	22
Noturus gyrinus	tadpole madtom	2		1	1		3	7
Lepomis gulosus	warmouth sunfish	1			1			2
Gambusia affinis	western mosquitofish	2		42		5	8	57
Pomoxis annularis	white crappie		1	1	1	3		6

Table 12- Known host fish associated with mussel species encountered in the Clear and Muddy Boggy rivers.

Mussel Species (scientific and common names)		Fish Host Species (scientific and common names)	
Potamilis purpuratus	Bluefer	*Aplodinotus grunniens*	Freshwater Drum
Truncilla truncata	Deertoe	*Aplodinotus grunniens*	Freshwater Drum
Lampsilis siliquoidea	Fatmucket	*Lepomis macrochirus*	Bluegill
		Lepomis megalotis	Longear Sunfish
		Micropterus salmoides	Largemouth bass
		Pomoxis annularis	White crappie
		Lepomis cyanellus	Green Sunfish
		Noturus gyrinus	Tadpole Madtom
		Pimephales notatus	Bluntnose minnow
		Notropis stramineus	Sand Shiner
Truncilla donaciformis	Fawnsfoot	*Aplodinotus grunniens*	Freshwater Drum
Leptodea fragilis	Fragile Papershell	*Lepomis cyanellus*	Green Sunfish
		Aplodinotus grunniens	Freshwater Drum
Quadrula quadrula	Mapleleaf	*Pylodictis olivaris*	Flathead catfish
Quadrula pustulosa	Pimpleback	*Ictalurus punctatus*	Channel catfish
		Pomoxis annularis	White crappie
		Pylodictis olivaris	Flathead catfish
Potamilis ohiensis	Pink Papershell	*Aplodinotus grunniens*	Freshwater Drum
		Pomoxis annularis	White crappie
Tritogonia verrucosa	Pistolgrip	*Pylodictis olivaris*	Flathead catfish
Lampsilis cardium	Plain Pocketbook	*Micropterus salmoides*	Largemouth bass
		Lepomis cyanellus	Green Sunfish
		Lepomis macrochirus	Bluegill
Quadrula apiculata	Southern Mapleleaf	NA	NA
Obliquaria reflexa	Threehorn Wartyback	NA	NA
Amblema plicata	Threeridge	*Aplodinotus grunniens*	Freshwater Drum
		Ictalurus punctatus	Channel catfish
		Lepisosteus platostomus	Shortnose gar

		Lepomis cyanellus	Green Sunfish
		Lepomis gulosus	Warmouth sunfish
		Lepomis macrochirus	Bluegill
		Micropterus salmoides	Largemouth bass
		Moxostoma duquesnei	Black redhorse
		Moxostoma erythrurum	Golden redhorse
		Notropis atherinoides	Emerald Shiner
		Percina caprodes	Logperch
		Pomoxis annularis	White crappie
		Pylodictis olivaris	Flathead catfish
Fusconaia flava	Wabash pigtoe	*Lepomis macrochirus*	Bluegill
		Pomoxis annularis	White crappie
Quadrula nodulata	Wartyback	*Ictalurus punctatus*	Channel catfish
		Lepomis macrochirus	Bluegill
		Micropterus salmoides	Largemouth bass
		Pomoxis annularis	White crappie
		Pylodictis olivaris	Flathead catfish
Megalonaias nervosa	Washboard	*Aplodinotus grunniens*	Freshwater Drum
		Dorosoma cepedianum	Gizzard Shad
		Ictalurus punctatus	Channel catfish
		Lepisosteus osseus	Longnose gar
		Lepomis macrochirus	Bluegill
		Lepomis cyanellus	Green Sunfish
		Lepomis megalotis	Longear Sunfish
		Lepomis gulosus	Warmouth sunfish
		Micropterus punctulatus	Spotted Bass
		Micropterus salmoides	Largemouth bass
		Notemigonus crysoleucas	Golden Shiner
		Noturus gyrinus	Tadpole Madtom
		Percina caprodes	Logperch
		Percina phoxocephala	Slenderhead Darter
		Pomoxis annularis	White crappie
		Pylodictis olivaris	Flathead catfish

Lasmingona complanata	White Heelsplitter	*Micropterus salmoides*	Largemouth bass
		Lepomis humilis	Orangespotted Sunfish
		Pomoxis annularis	White crappie
		Lepomis cyanellus	Green Sunfish
Lampsilis teres	Yellow Sandshell	*Cyprinella venusta*	Blacktail Shiner
		Lepisosteus osseus	Longnose gar
		Lepisosteus platostomus	Shortnose gar
		Lepomis macrochirus	Bluegill
		Lepomis cyanellus	Green Sunfish
		Lepomis humilis	Orangespotted Sunfish
		Lepomis gulosus	Warmouth sunfish
		Micropterus salmoides	Largemouth bass
		Pomoxis annularis	White crappie

Table 13- Relative abundance (proportion of an individual species relative to all other species captured) of fish host species collected during fish sampling. Site codes are described in Figure 2.

Species	Common name	MB1	MB2	MB5	CB1	CB3	CB5
Lepomis macrochirus	bluegill	0.0560	0.0968	0.1954	0.1747	0.0636	0.0685
Etheostoma chlorosomum	bluntnose darter				0.0044		
Pimephales notatus	bluntnose minnow	0.0407		0.1540	0.0524	0.0355	0.0102
Ictalurus punctatus	channel catfish	0.0305	0.0645	0.0115	0.0480	0.0374	0.1320
Notropis atherinoides	emerald shiner			0.0023		0.0019	
Pylodictis olivaris	flathead catfish		0.0323		0.0044		0.0076
Aplodinotus grunniens	freshwater drum	0.0076			0.0044		
Dorosoma cepedianum	gizzard shad	0.0025				0.0019	
Moxostoma erythrurum	golden redhorse			0.0023			
Notemigonus crysoleucas	golden shiner					0.0056	
Lepomis cyanellus	green sunfish			0.0851	0.0437	0.0019	0.0152
Micropterus salmoides	largemouth bass	0.0051	0.0323	0.0092	0.0262	0.0019	
Percina caprodes	logperch	0.0025					
Lepomis megalotis	longear sunfish	0.0051	0.3226	0.0253	0.0873	0.0037	0.0863
Lepisosteus osseus	longnose gar	0.0280	0.0323			0.0243	0.0102
Lepomis humilis	orangespotted sunfish	0.3282		0.1080	0.1135	0.0430	
Notropis stramineus	sand shiner	0.2316		0.0460	0.1179	0.0056	0.0152
Lepisosteus platostomus	shortnose gar	0.0051			0.0044		
Percina phoxocephala	slenderhead darter				0.0087	0.0112	0.0025
Micropterus punctulatus	spotted bass	0.0025		0.0023	0.0175		0.0127
Noturus gyrinus	tadpole madtom	0.0051		0.0023	0.0044		0.0076
Lepomis gulosus	warmouth sunfish	0.0025			0.0044		
Pomoxis annularis	white crappie		0.0323	0.0023	0.0044	0.0056	

Table 14- Species and mussel bed presence matrix of *r*-values for Spearman's rank correlation coefficient of abiotic factors. Values of 0.70 or more are considered multicollinear for landscape analyses and indicated below by asterisks. Variables are: WD= width to depth ratio, HEL= proportion of highly erodible land, Geo= proportion of shale, Rip= riparian corridor width, Land= proportion of agriculture/pasture land, Forest= proportion of forested vegetation, Sin= sinuosity, and Drain= drainage area.

	HEL	Geo	Rip	Land	Forest	Sin	Drain
WD	0.07	-0.05	0.10	-0.11	0.03	-0.04	0.15
HEL		0.33	-0.29	0.47	-0.20	-0.28	-0.26
Geo			-0.24	0.34	-0.03	-0.24	-0.60
Rip				-0.86*	0.83*	0.13	0.62
Land					-0.78*	-0.31	-0.67
Forest						0.22	0.37
Sin							0.20

Table 15- Species density matrix of *r*-values for Spearman's rank correlation coefficient of abiotic factors. Values of 0.70 or more are considered multicollinear for landscape analyses and indicated below by asterisks. Variables are: WD= width to depth ratio, HEL= proportion of highly erodible land, Geo= proportion of shale, Rip= riparian corridor width, Land= proportion of agriculture/pasture land, Forest= proportion of forested vegetation, Sin= sinuosity, and Drain= drainage area.

	HEL	Geo	Rip	Land	Forest	Sin	Drain
WD	-0.73*	-0.64	0.51	-0.77*	0.49	0.19	0.55
HEL		0.74*	-0.50	0.83*	-0.36	-0.62	-0.71*
Geo			-0.51	0.70*	-0.18	-0.30	-0.64
Rip				-0.79*	0.88*	0.25	0.67
Land					-0.73*	-0.45	-0.84*
Forest						0.13	0.53
Sin							0.41

Table 16- Model ranking of mussel bed presence competing hypotheses. *K* is the number of estimable parameters, AICc is AIC corrected for small sample size, Δi = AICc differences, *wi* = Akaike weights, and Log is the log likelihood. Models are listed in descending order from top- to lowest -ranked model (top ranked models $\Delta i \leq 2$, represented by an asterisk). A "+" indicates the covariates are additive in the model. Drain= drainage area, Land= proportion of agriculture/pasture land, HEL= proportion of highly erodible land, Rip= riparian corridor width, Bank= bank erodibility, Geo= proportion of shale, and Sin= sinuosity.

Model	Description	*K*	AICc	Δ_i	w_i	Log
M1*	Drain+Land	3	62.61	0.00	0.32	-27.99
M4*	Drain+HEL+Land	4	62.66	0.05	0.31	-26.79
M3*	Rip+Bank+HEL	5	62.86	0.25	0.28	-25.60
M2	Drain+Geo+Sin	4	65.23	2.62	0.09	-28.07

Table 17- Model ranking of species presence competing hypotheses. *K* is the number of estimable parameters, AICc is AIC corrected for small sample size, Δi = AICc differences, *wi* = Akaike weights, and Log is the log likelihood. Models are listed in descending order from top- to lowest-ranked model (top ranked models $\Delta i \leq 2$, represented by an asterisk). A "+" indicates the covariates are additive in the model. Drain= drainage area, HEL= proportion of highly erodible land, WD= width to depth ratio, Rip= riparian corridor width, Geo= proportion of shale, Land= proportion of agriculture/pasture land, Forest= proportion of forest vegetation, and Bank= bank erodibility.

Species	Model	Description	*K*	AICc	Δ_i	w_i	Log
Bleufer	M2*	Drain+WD	3	31.44	0.00	0.70	-12.15
	M4	Geo+Land+WD	4	34.70	3.26	0.14	-12.35
	M3	Drain+HEL	3	35.27	3.83	0.10	-14.06
	M1	HEL+Rip	3	36.50	5.07	0.06	-14.68
Fragile papershell	M1*	Drain+Rip	3	34.65	0.00	0.78	-13.75
	M3	Drain+WD+HEL	4	37.53	2.88	0.18	-13.76
	M4	Drain+Sin+HEL	4	41.37	6.72	0.03	-15.69
	M2	Rip+HEL+Bank	5	43.08	8.43	0.01	-14.96
Pimpleback	M1*	Drain	2	34.89	0.00	0.45	-15.17

	M4*	Drain+HEL+Bank	4	35.80	0.91	0.28	-12.90
	M2*	Geo+Forest	3	36.08	1.19	0.25	-14.47
	M3	Drain+Geo+WD	5	41.07	6.17	0.02	-13.95
Wabash pigtoe	M3*	Rip+Land	3	32.31	0.00	0.94	-12.58
	M1	Land	2	38.97	6.66	0.03	-17.21
	M2	Drain+Rip	3	39.85	7.54	0.02	-16.35
	M4	HEL+Land+Bank	5	43.76	11.45	0.00	-15.30

Table 18- Model ranking of species density competing hypotheses. *K* is the number of estimable parameters, AICc is AIC corrected for small sample size, Δi = AICc differences, *wi* = Akaike weights, and Log is the log likelihood. Models are listed in descending order from top- to lowest-ranked model (top ranked models $\Delta i \leq 2$, represented by an asterisk). A "+" indicates the covariates are additive in the model. Drain= drainage area, WD= width to depth ratio, Rip= riparian corridor width, Geo= proportion of shale, Land= proportion of agriculture/pasture land, Forest= proportion of forest vegetation, Sin= sinuosity, and Sub= substrate.

Species	Model	Description	*K*	AICc	Δ_i	w_i	Log
Bleufer	M2*	Drain+WD	4	66.49	0.00	0.36	-25.24
	M1*	Drain+Rip	4	66.66	0.17	0.33	-25.33
	M3*	Geo+Sub	4	66.81	0.33	0.31	-25.41
	M4	Drain+Sin+Geo	5	75.62	9.13	0.00	-25.31
Fragile papershell	M2*	Geo+WD	4	68.26	0.00	0.37	-26.13
	M1*	Drain+Geo	4	68.41	0.15	0.35	-26.21
	M3*	Drain+WD	4	68.89	0.63	0.27	-26.45
	M4	Drain+WD+Geo	5	77.25	8.98	0.00	-26.12
Pimpleback	M1*	Drain	3	65.84	0.00	0.88	-27.92
	M3	Geo+Forest	4	70.79	4.95	0.07	-27.39

	M2	Drain+Geo	4	71.72	5.88	0.05	-27.86
	M4	Drain+Forest+Sub	5	79.57	13.73	0.00	-27.28
Wabash pigtoe	M1*	Land	3	77.14	0.00	0.94	-33.57
	M2	WD+Rip	4	82.56	5.42	0.06	-33.28
	M3	Forest+WD+Sub	5	92.51	15.37	0.00	-33.76

Table 19- Total number of PIT tagged mussels at our four sample sites. Species A has heavy ornamented or obese shells. Species B has light smooth shells. Sites codes described in Figure 2.

Species A	Species B	MB1	MB4	CB1	CB5	Total
Bleufer		33	18	31	2	84
Threeridge		13	28	21	4	66
	Fragile papershell	24	2	15	4	45
	Wabash pigtoe	0	5	0	26	31
	Yellow sandshell	16	13	19	12	60
Total		86	66	86	48	286

Table 20- Mean species length, height, width (1 cm), and weight (1 g) by sampling site. Range in parentheses. Sites codes described in Figure 2.

Site	Species	Length (cm)	Height (cm)	Width (cm)	Weight (g)
MB1	Bleufer	119 (86-175)	78 (55-110)	55 (39-71)	345 (124-958)
	Fragile papershell	99 (66-120)	62 (40-83)	37 (22-45)	113 (28-167)
	Threeridge	155 (112-201)	105 (75-130)	67 (46-160)	768 (319-1131)
	Yellow sandshell	93 (63-120)	45 (31-58)	35 (20-50)	101 (28-193)
MB4	Bleufer	131 (100-166)	84 (63-110)	56 (43-70)	415 (175-761)
	Fragile papershell	106 (100-111)	66 (61-71)	45 (41-49)	155 (132-178)
	Threeridge	113 (44-234)	79 (34-140)	49 (20-81)	323 (22-1647)
	Yellow sandshell	99 (55-112)	47 (27-53)	36 (16-46)	120 (14-171)
	Wabash pigtoe	79 (57-99)	64 (49-74)	43 (33-49)	142 (49-230)
CB1	Bleufer	112 (83-141)	72 (57-88)	51 (37-67)	264 (115-482)
	Fragile papershell	87 (34-110)	57 (40-75)	37 (25-81)	84 (32-161)
	Threeridge	102 (65-175)	75 (51-127)	49 (34-63)	308 (76-1103)
	Yellow sandshell	100 (59-118)	47 (27-55)	38 (18-47)	116 (19-188)
CB5	Bleufer	82 (71-92)	53 (42-63)	38 (29-46)	112 (65-158)
	Fragile papershell	63 (45-76)	40 (26-49)	24 (15-30)	38 (11-57)
	Threeridge	71 (50-113)	52 (38-81)	30 (18-50)	121 (26-360)
	Yellow sandshell	87 (61-102)	41 (29-47)	30 (19-38)	78 (22-133)
	Wabash pigtoe	57 (36-84)	45 (27-62)	29 (21-45)	58 (24-186)

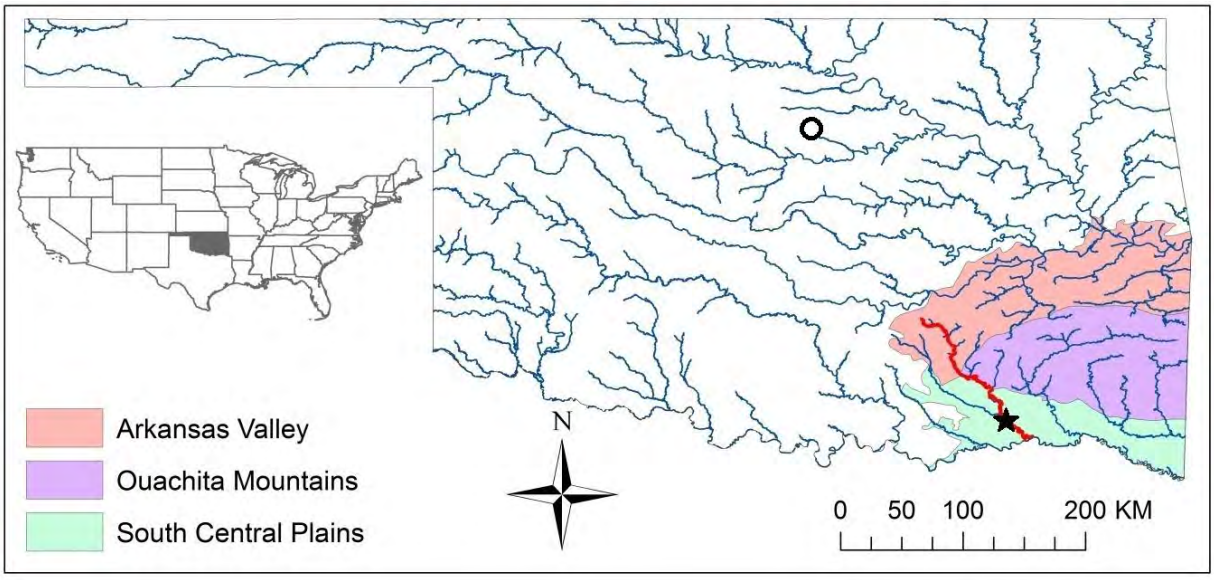

Figure 1- Lake McMurtry (identified with an open circle) is the reservoir where sidescan sonar key images were developed using scans of placed mussel shells. The Muddy Boggy River traverses three major ecoregions (Arkansas Valley, Ouachita Mountains, and the South Central Plains). The 32-km study reach (identified with a star) was located in the South Central Plains ecoregion.

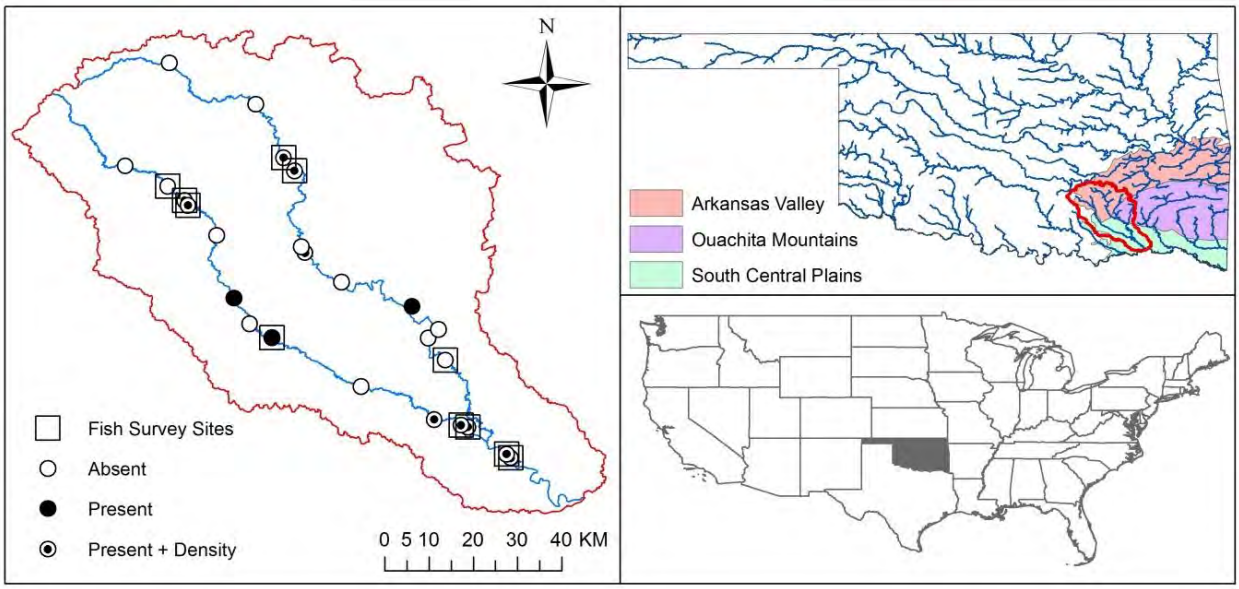

Figure 2- Sampling site locations on the Muddy Boggy and Clear Boggy rivers. The Muddy Boggy River is the easternmost stream and sites are from downstream to upstream: MB1 – MB13. The Clear Boggy River is the westernmost stream and sites are from downstream to upstream: CB1 – CB12.

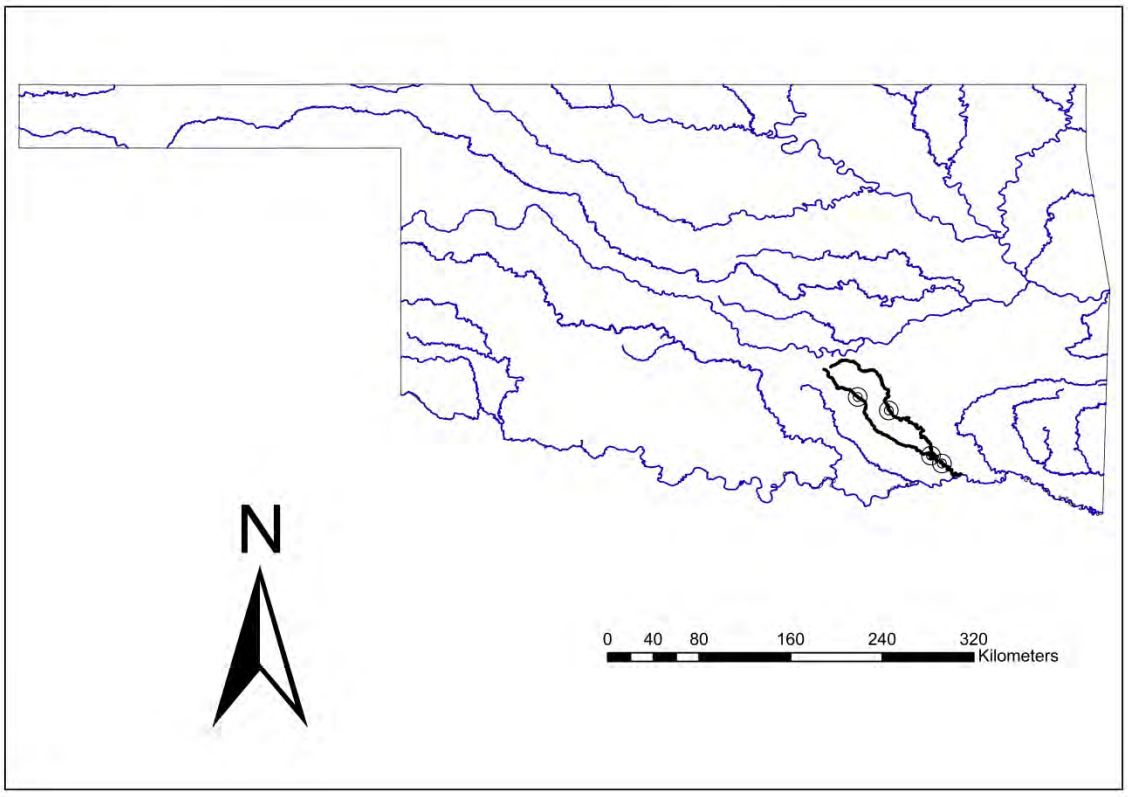

Figure 3- PIT tagged mussel sampling site locations in the Muddy Boggy and Clear Boggy rivers. The Muddy Boggy River is the easternmost stream and sites are from downstream to upstream: MB1 and MB4. The Clear Boggy River is the westernmost stream and sites are from downstream to upstream: CB1 and CB5.

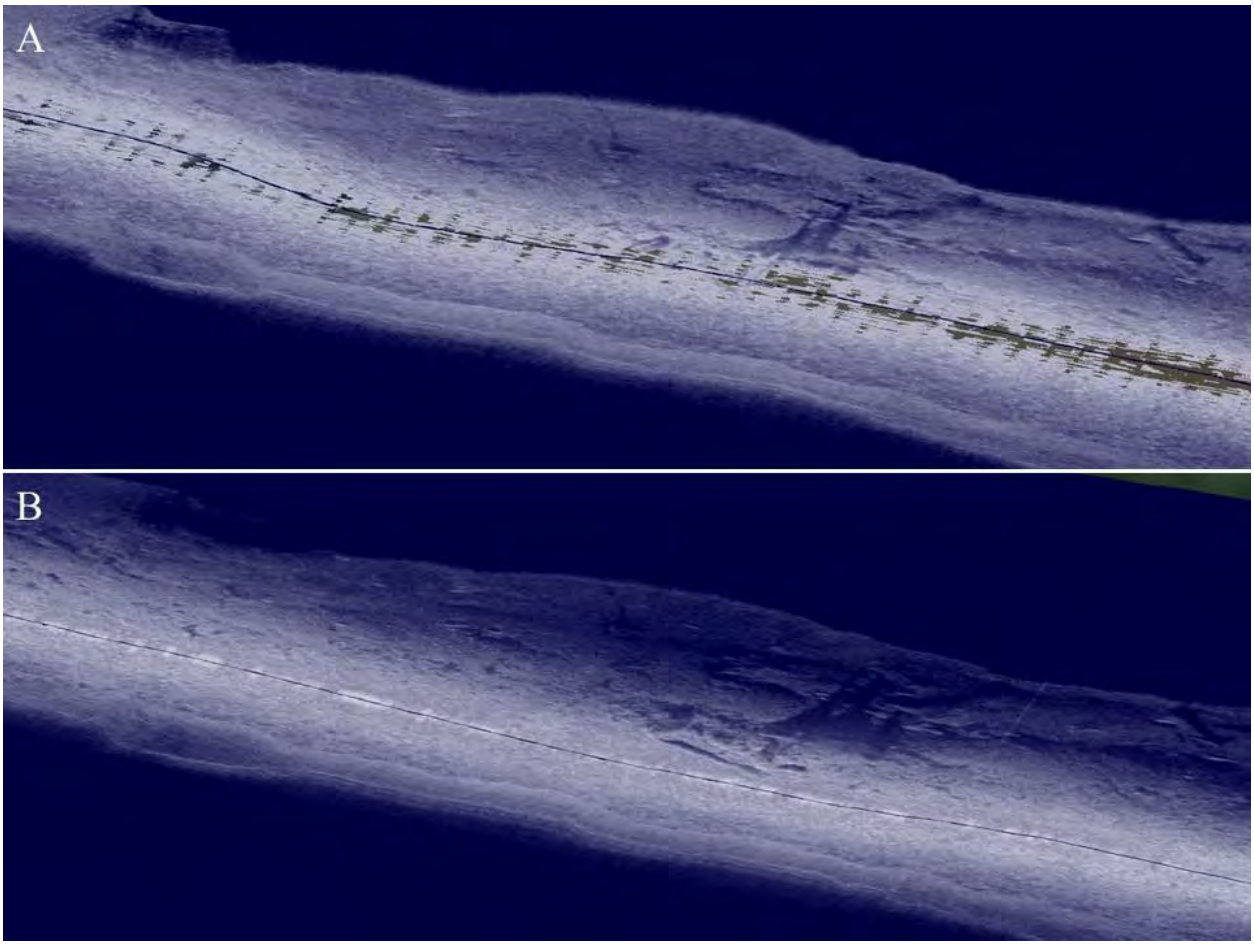

Figure 4- Sidescan images of a selected area using two different frequencies for image capture. A) image captured at a frequency of 455 kHz and B) image captured at a frequency of 800 kHz.

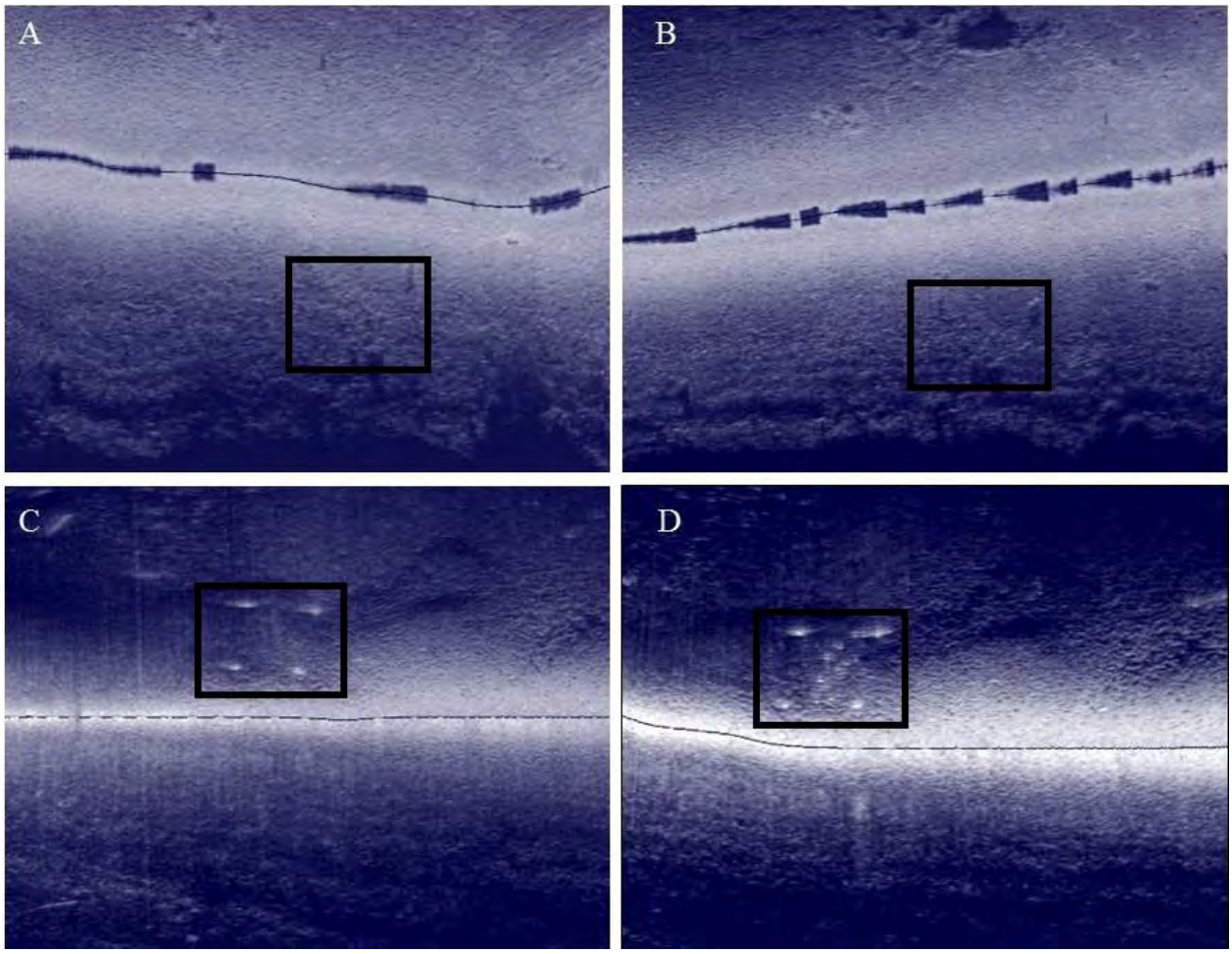

Figure 5- Sidescan images of a 9-m^2 area (black rectangle) containing: A) coarse substrate with no mussel shells, B) coarse substrate with mussel shells, C) fine substrate with no mussel shells, and D) fine substrate with mussel shells. The four white images in Panel C and D are reflectance from T bars outlining the sample area.

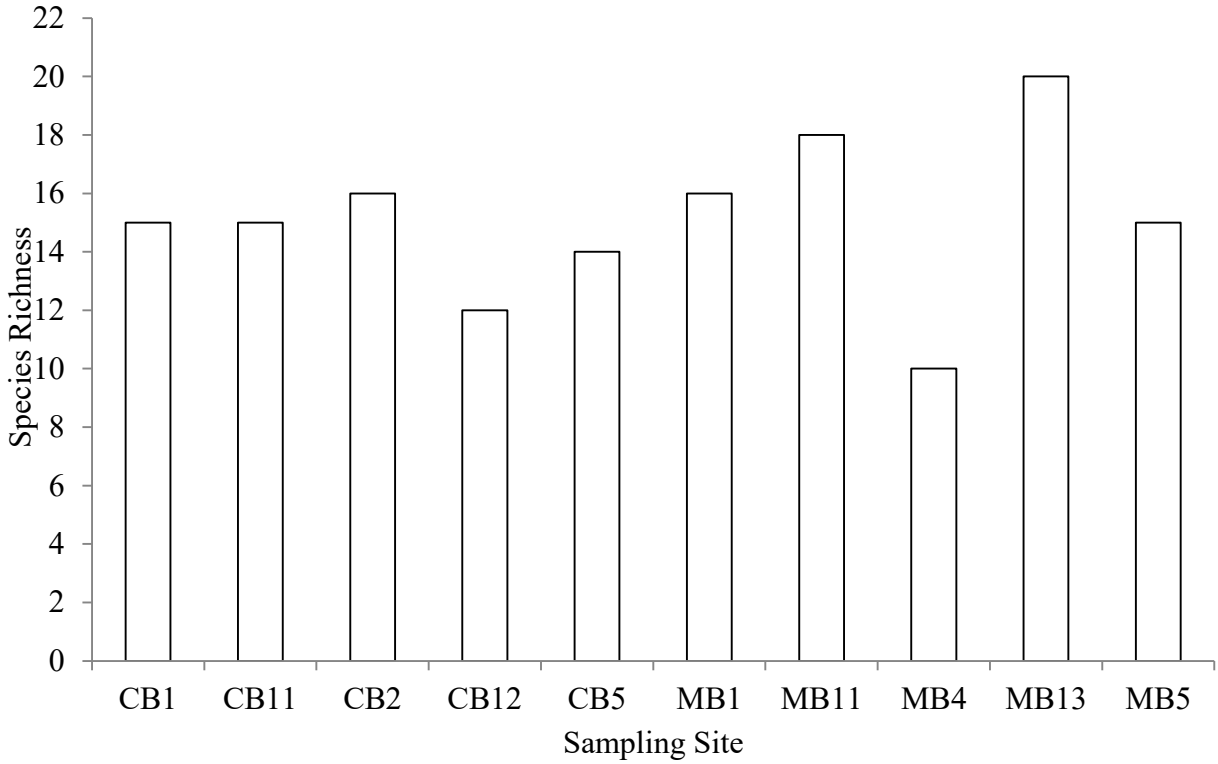

Figure 6- Mussel species richness by site on the Muddy and Clear Boggy rivers. Study site names described in Figure 2.

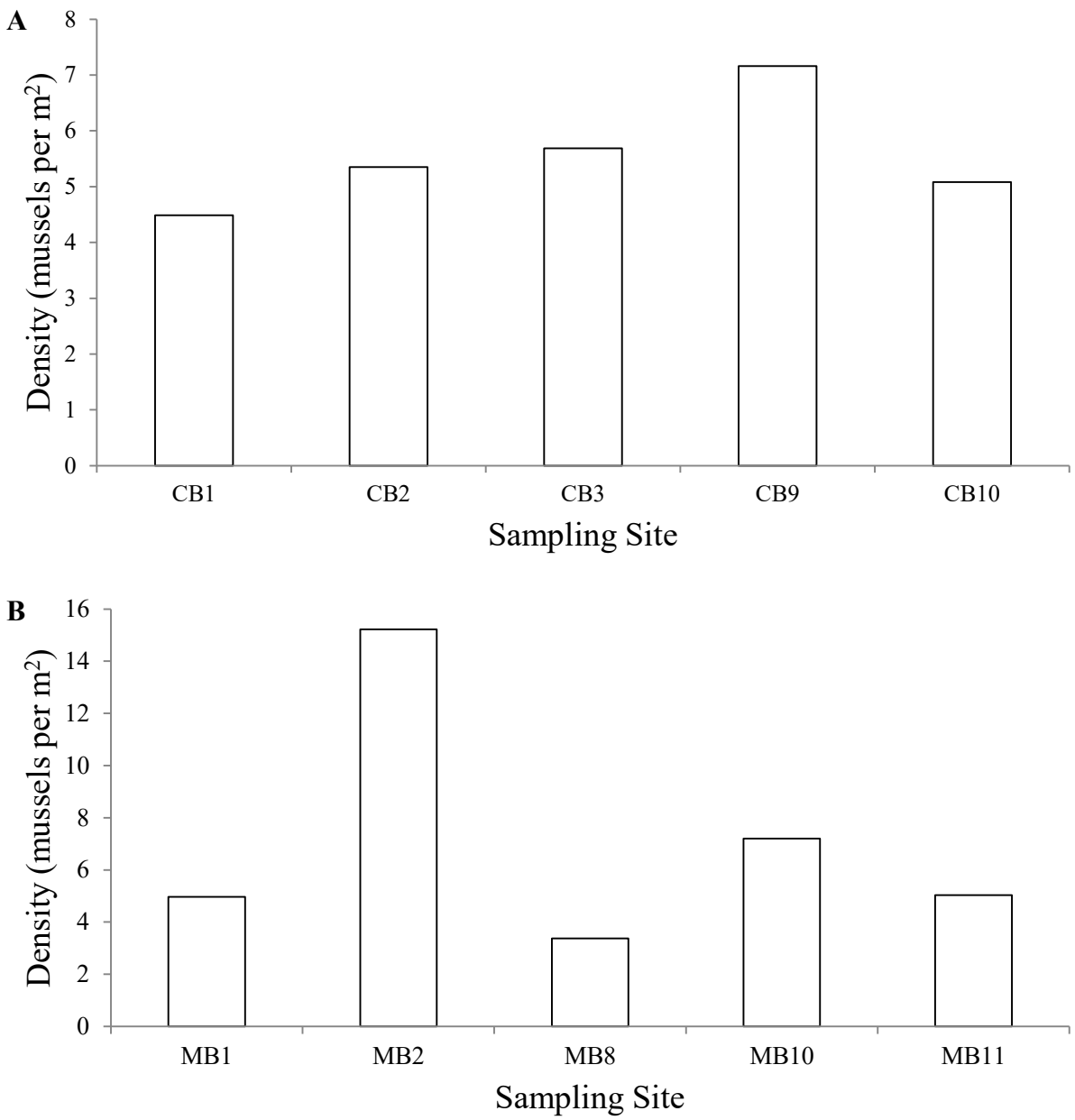

Figure 7- Mussel density (per m^2) by site on the Clear Boggy (A) and Muddy Boggy (B) rivers. Study site names were described in Figure 2.

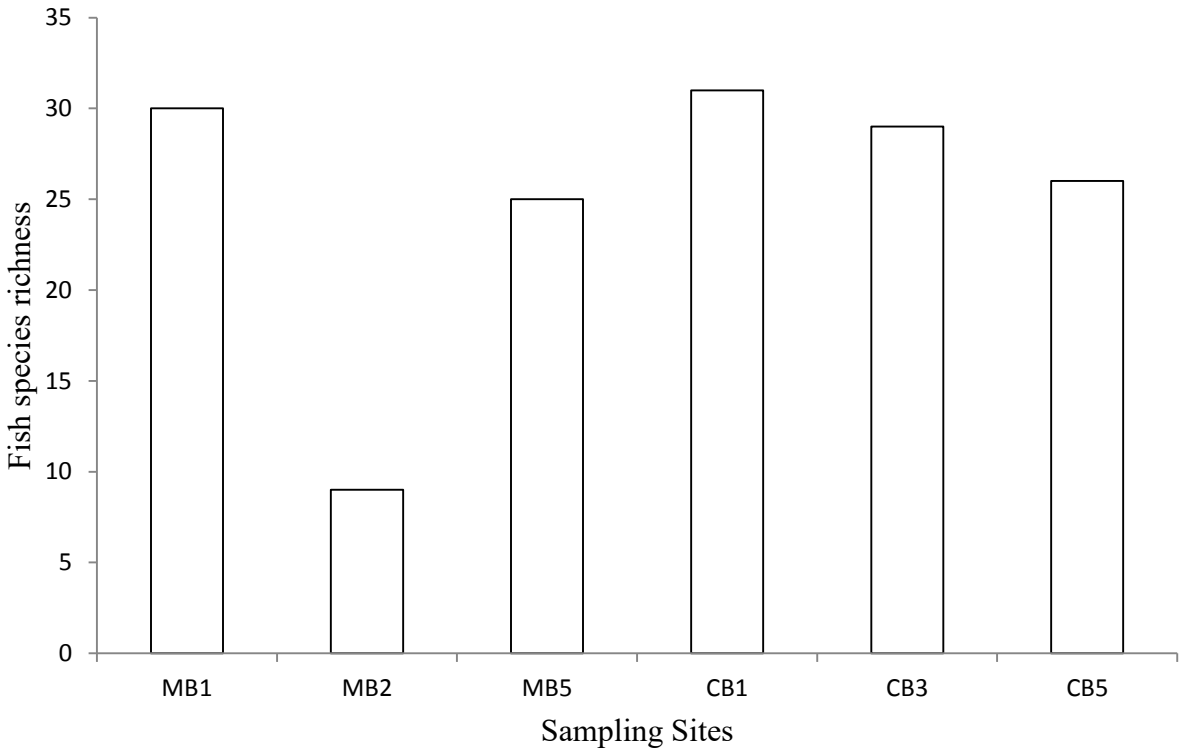

Figure 8- Fish species richness by site on the Muddy and Clear Boggy rivers. Study site names described in Figure 2.

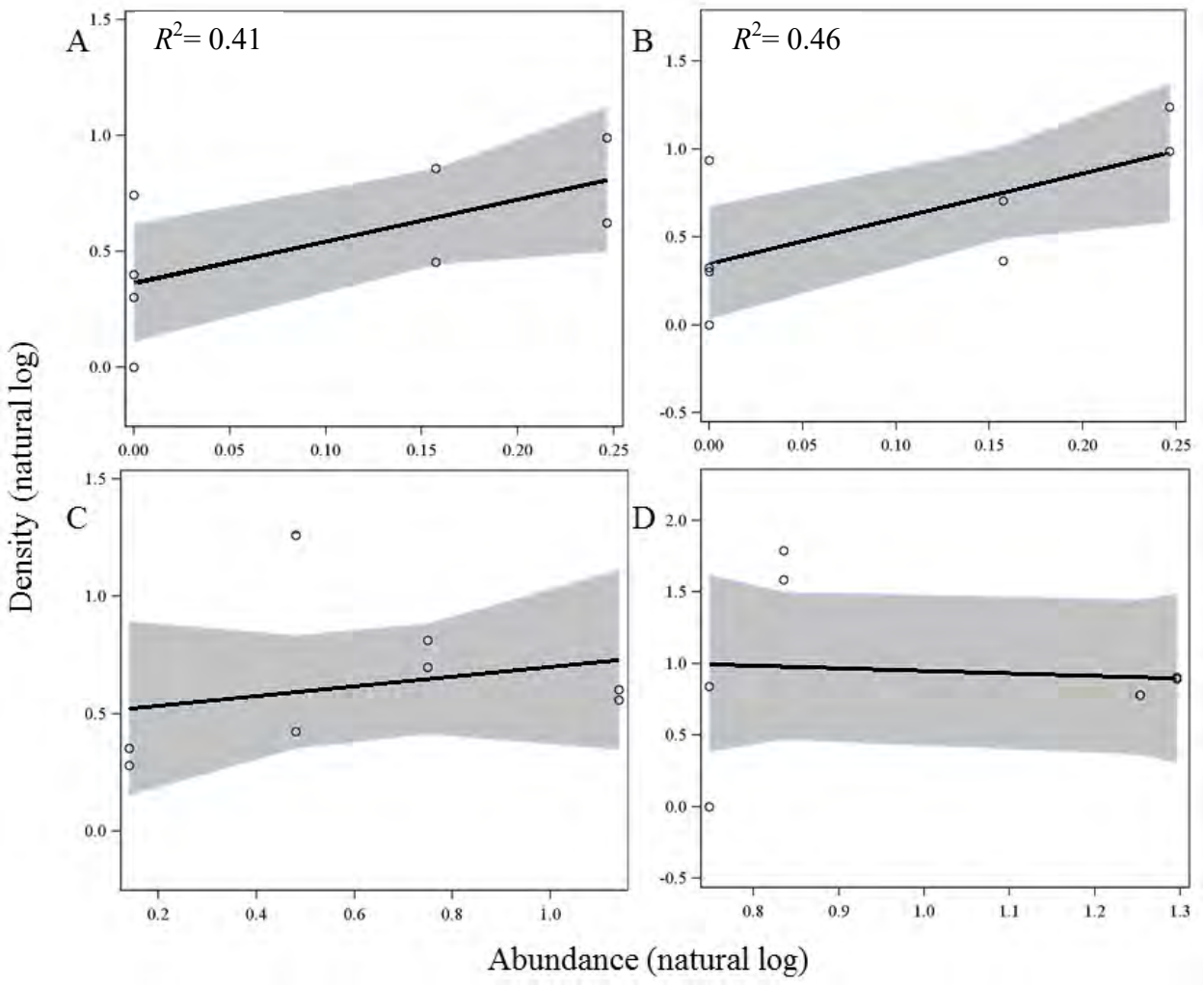

Figure 9- Linear regression relating species density (10 m^2) to fish-host abundance. Open circles represent data points, solid lines represent fitted regression line, and shaded areas represent confidence limits (90%). Regression models are for: A= bleufer (positive relationship), B= fragile papershell (positive relationship), C= pimpleback, and D= Wabash pigtoe.

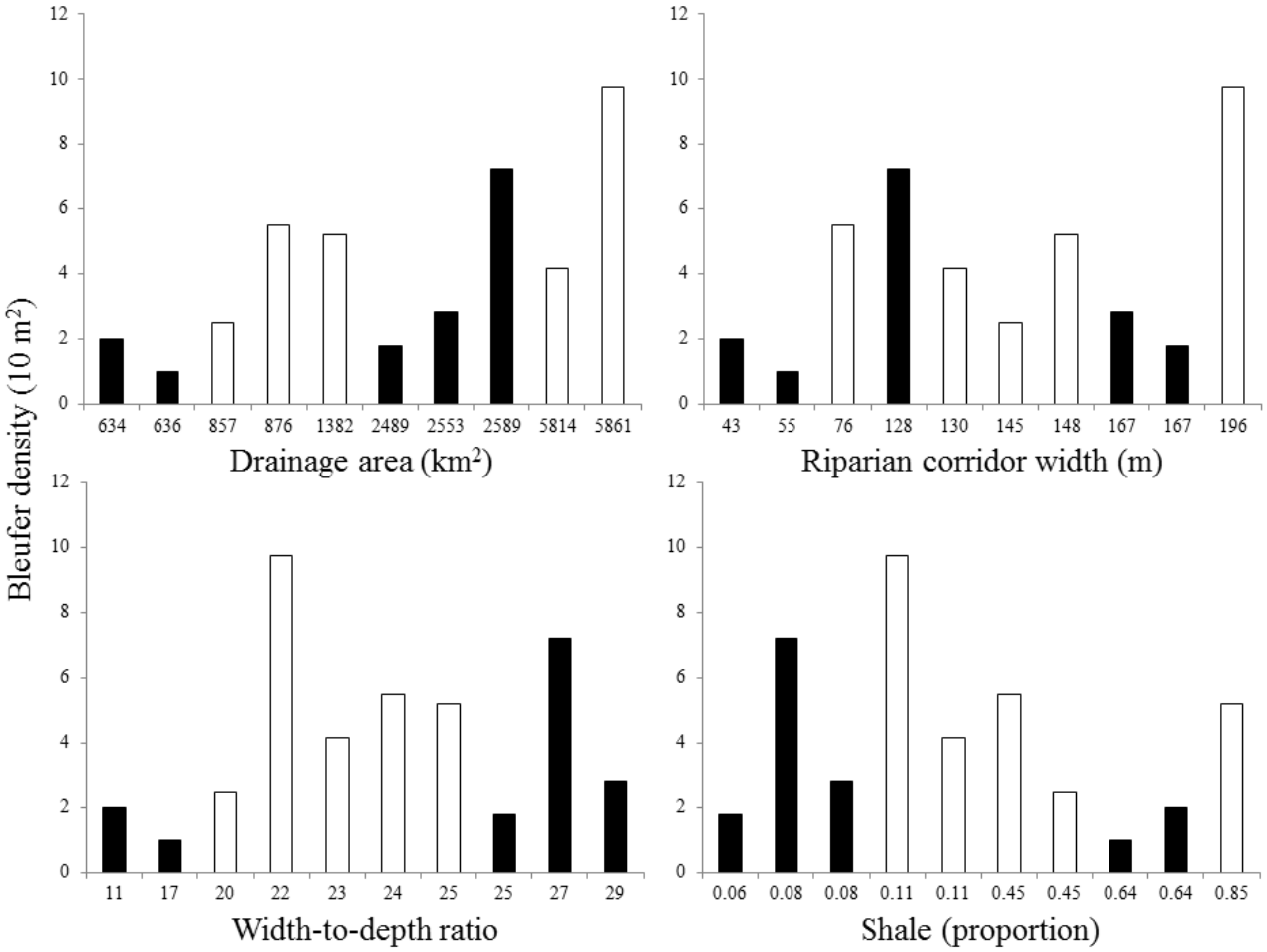

Figure 10- The relationship between bleufer density and drainage area, riparian corridor width, width-to-depth ratio, and shale. Each bar represents one sample location with black bars associated with samples from the Clear Boggy River and white bars with samples from the Muddy Boggy River.

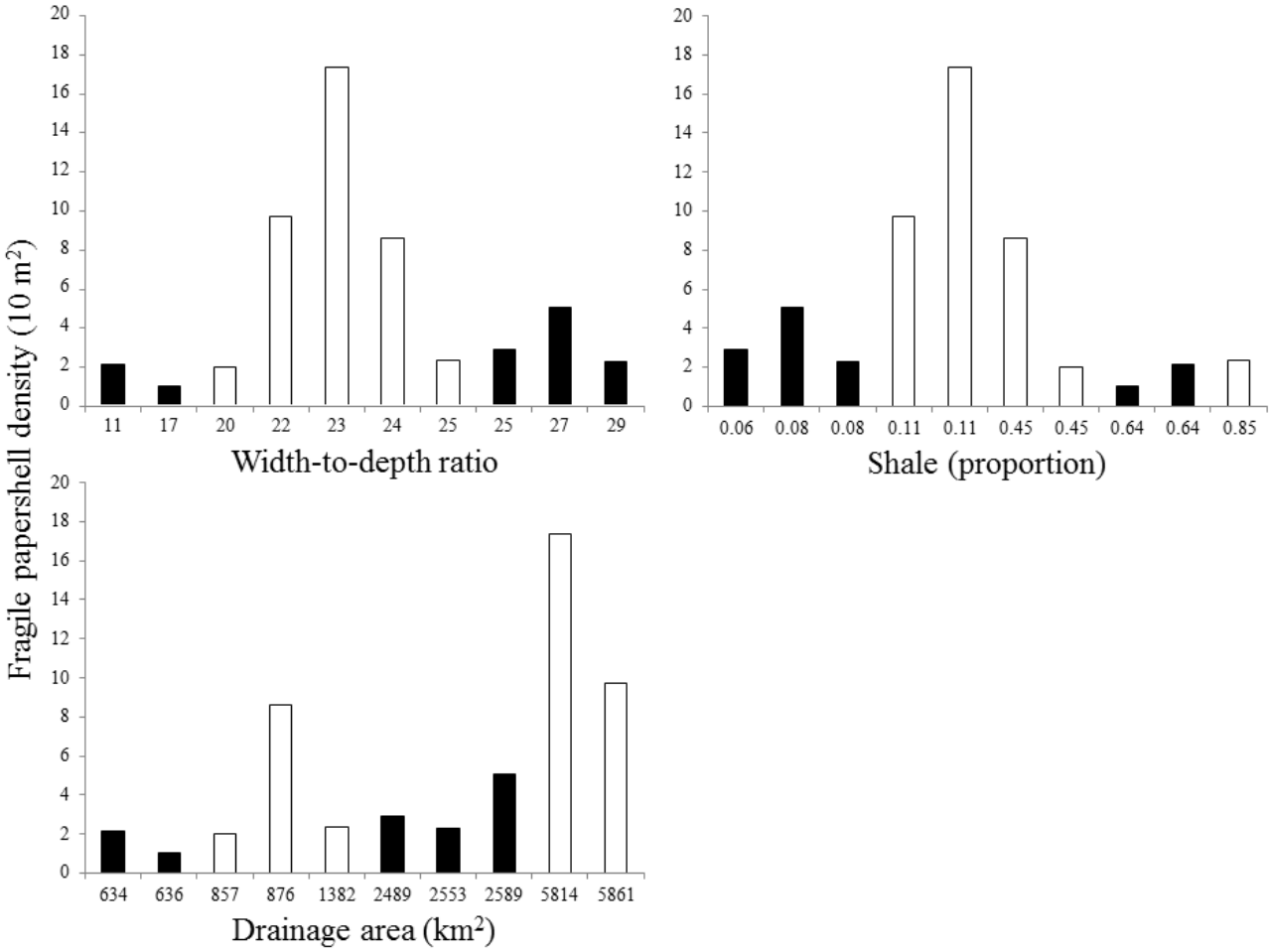

Figure 11- The relationship between fragile papershell density and width-to-depth ratio, shale, and drainage area. Each bar represents one sample location with black bars associated with samples from the Clear Boggy River and white bars with samples from the Muddy Boggy River.

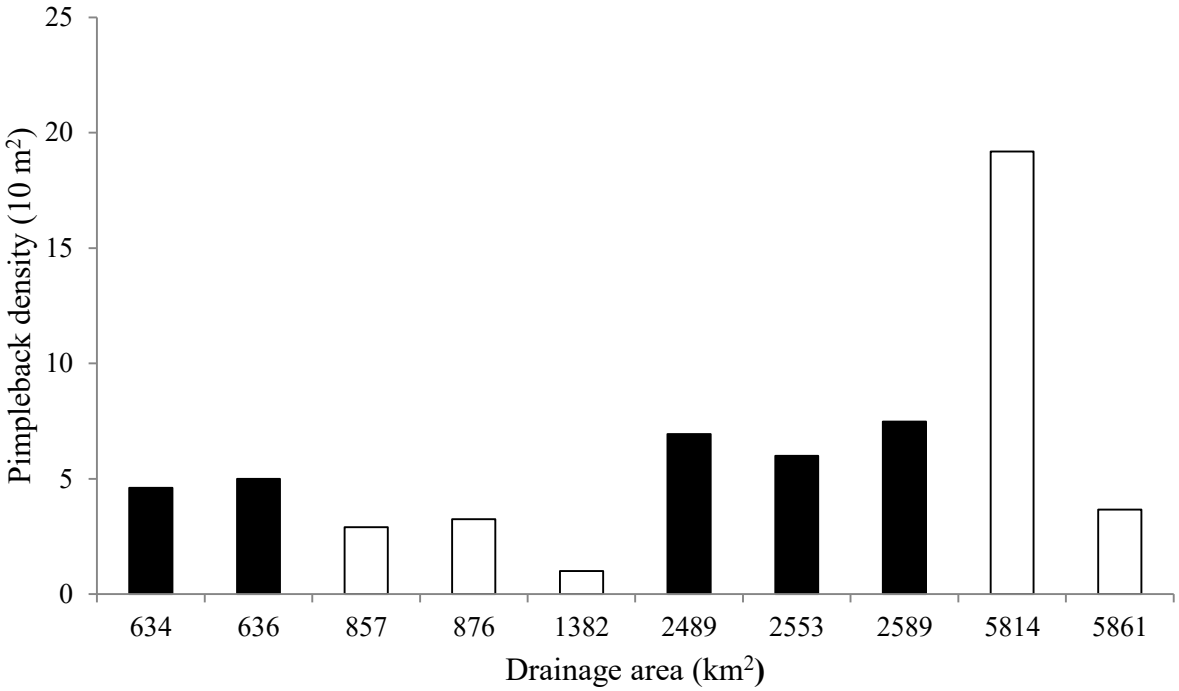

Figure 12- The relationship between pimpleback density and drainage area at each sample site. Each bar represents one sample location with black bars representing samples from the Clear Boggy River and white bars representing samples from the Muddy Boggy River.

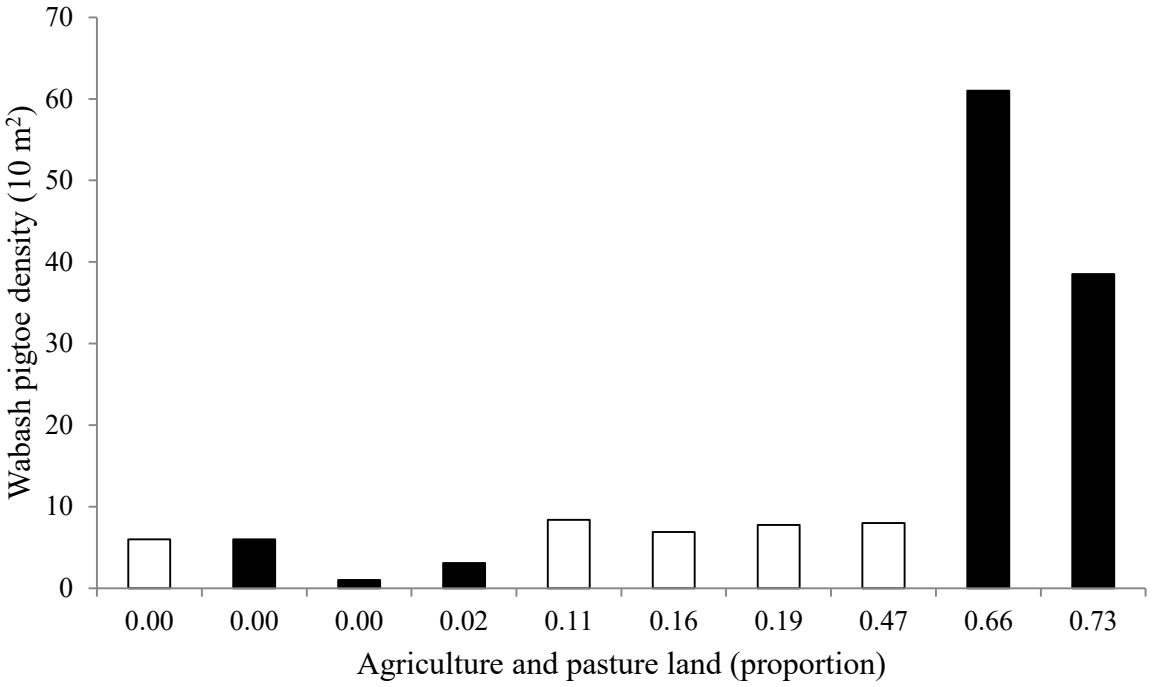

Figure 13- The relationship between Wabash pigtoe density and agriculture and pasture land at each study site. Each bar represents one sample location with black bars representing samples from the Clear Boggy River and white bars representing samples from the Muddy Boggy River.

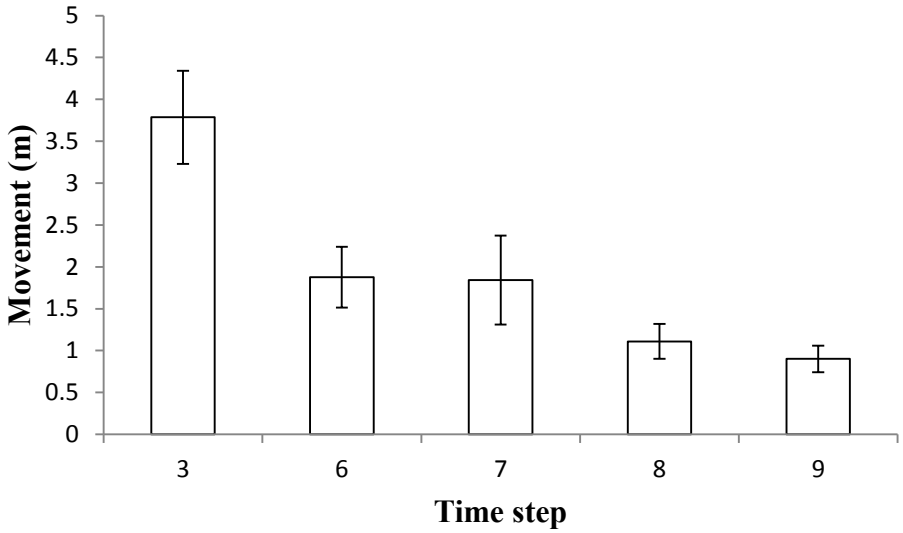

Figure 14- Mean distance (90% confidence limits) moved by freshwater mussels at different time steps. Time steps are: 3-March 2013; 6-July 2013; 7-August 2013; 8-September 2013; 9-October 2013.

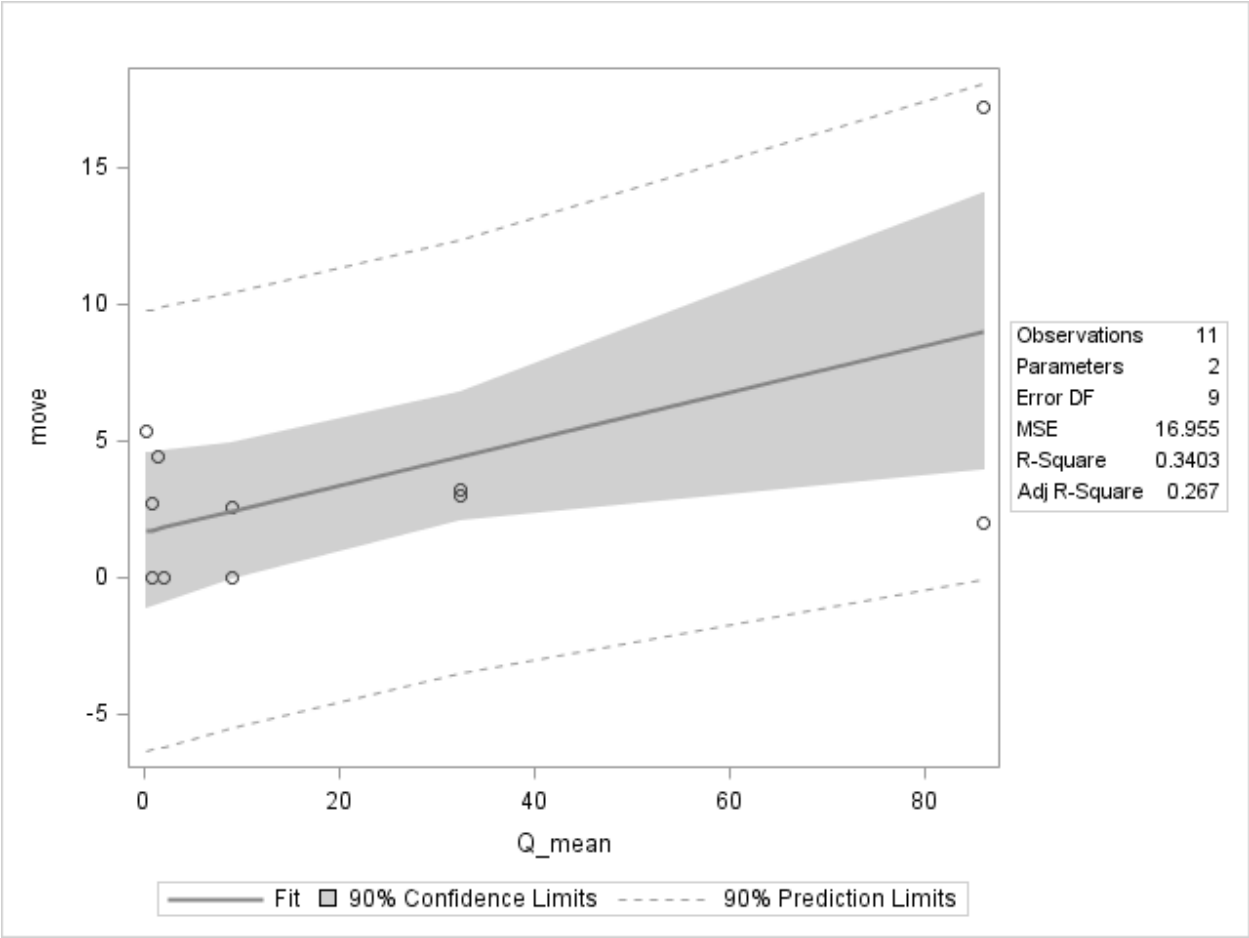

Figure 15- Mean distance (90% confidence limits) moved (m) by fragile papershell with changing mean discharge. Mean discharge was calculated as the mean between the relocation event and the previous relocation event.