FACTORS RELATED TO THE DISTRIBUTION OF FRESHWATER MUSSELS ON MUDDY AND CLEAR BOGGY RIVERS

By

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Bachelor of Science in Natural Resource Ecology and Management

Oklahoma State University

Stillwater, Oklahoma

2011

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 2016

FACTORS RELATED TO THE DISTRIBUTION OF FRESHWATER MUSSELS ON MUDDY AND CLEAR BOGGY RIVERS

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ACKNOWLEDGEMENTS

I would like to acknowledge numerous people who contributed to my Master's degree. My advisor, Shannon Brewer, helped me immensely through this learning endeavor and helped me to become a better scientist, writer, leader, and much more. Many others have assisted with the completion of thesis work which wouldn't have been possible without their help.

Shannon Brewer has been the most influential person to me becoming a scientist and expecting more out of myself. I can honestly say that if it was not for her patience and wanting to see me succeed that I may have never finished. She continually pushed me to do and be better. Most of all, Shannon continued support me in completing my thesis.

My committee members, Dan Shoup and Carla Goad provided useful insight to my project and to my knowledge of science in general. They assisted me with numerous questions related to my project and never minded taking time out of their day to sit down and talk with me.

Several professors and peers have contributed to my success. I want to thank my lab mates Bob Mollenhauer and Joey Dyer for assisting me in many ways from field assistance to statistics guidance. I also want to thank Tom Worthington, Jim Long, and Mark Gregory for providing valuable input.

I want to thank the technicians that help me with field and lab work. Mark Jensen and Bryce Burkehead worked hard with me that first summer in what was certainly one of the hottest summers on record. I want to thank Daniel Beatie for his hard work during a full season of field and lab work. I especially want to thank Thomas Campbell who worked on this project nearly as long as me and without who this would not have been possible.

Lastly, I want to acknowledge my family. I thank my wife, Kelli Powers for working to support our family while I was in school and for always being by my side through the good and the bad. I thank my daughter, Leah Powers for understanding that I could not always be there, but knowing she means the world to me.

This research is a contribution of the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey, Oklahoma Department of Wildlife Conservation, Oklahoma State University, and Wildlife Management Institute cooperating). Project funding was provided by the Oklahoma Department of Wildlife Conservation (F11AF00027).

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Date of Degree: MAY, 2016

Title of Study: FACTORS RELATED TO THE DISTRIBUTION OF FRESHWATER MUSSELS ON MUDDY AND CLEAR BOGGY RIVERS

Major Field: NATURAL RESOURCE ECOLOGY AND MANAGMENT

Abstract: Freshwater mussels play an important role in proper functioning river systems; however, worldwide, this group of freshwater taxa is one of the most imperiled. To implement effective conservation efforts, a better understanding of the factors related to the distribution and abundance of mussels is needed. The goal of this project was to determine the environmental factors related to the distribution and abundance of mussels in the Muddy and Clear Boggy rivers in southern Oklahoma. My objectives were: 1) determine the usefulness of side-scan sonar as a tool to locate freshwater mussels and 2) evaluate the environmental factors at multiple spatial scales that influence mussel distribution and abundance. First, side-scan sonar was used to develop reference images of mussels and then used to compare a 32 km reach of the Muddy Boggy River. Results confirmed that ~80% of sites had mussels or shells present. I determined that side-scan sonar was an effective tool for preliminary assessments of mussel presence when they are located at substrate surface and in relatively fine substrate. Side-scan sonar data were then combined with additional survey data to build models predicting mussel-bed locations, species presence, and species densities. Generally, my predictions of mussel-bed locations had poor predictive power, probably due to the dispersed nature of mussel beds in both rivers. Hypothesis explaining relationships between landscape and inchannel factors and species densities were evaluated with mixed results. Some models predicting species densities were poor predictors (e.g., bleufer) whereas other models explained > 40% of the variation in my observed data (e.g., Wabash pigtoe, fragile papershell). Models predicting freshwater mussel densities performed much better than presence models with drainage area, width:depth ratios, and percent of shale geology selected most often as explanatory variables. Unlike many species, Wabash pigoe was tolerant of agriculture land use. Mussel species with few host fishes showed significant positive relationships between mussel density and fish-host density. The results of my 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.

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CHAPTER I

INTRODUCTION

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), we continue to struggle in understanding: 1) habitat suitability, 2) how to identify successful mussel relocation and introduction sites, and 3) distributions and population dynamics of individual species (Haag and Williams 2014). 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., release 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. 2011, Bódis et al. 2014).

Declines in freshwater mussel populations relate to several abiotic and biotic factors associated with landscape change: habitat destruction (e.g., conversion of forest and prairies to agriculture and pasture land; Box and Mossa 1999), water-quality degradation (e.g., runoff containing increased amounts of fertilizers and pesticides; Carpenter et al. 1998), hydrologic change (e.g., dam construction; Watters 1996), and loss 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). Habitat degradation is linked to loss of freshwater mussel diversity and abundance (Osterling et al. 2010). Conversion of forest and prairies to agriculture and pasture lands can 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 2006). To further exacerbate the situation, climate change is expected to alter precipitation and temperature patterns (Girvetz et al. 2009) that could further reduce mussel richness and distributions 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). Understanding how factors relate across spatial scales to influence mussel distributions and abundances is important for effective conservation efforts including choices of reintroduction or restoration sites.

One factor that has hindered the advancement of landscape models in prairie streams is the difficulty of sampling freshwater mussels in these systems. Traditionally, many freshwater mussel surveys focused on Clearwater streams and consisted of wading or walking along the stream bank using visual searches (Hoggarth 1992, Watters 1994b, Christian and Harris 2005). Visual searches were problematic as nearly 80% of a mussel population may occupy deep water or be buried in the substrate (Smith et al. 2000, McAlpine and Sollows 2014). Deep streams, especially those in turbid systems, require the use of an underwater breathing apparatus (Christian and Harris 2005). Incorporating SCUBA is challenging as the divers need extensive training and certifications. Additionally, diving carries its own risks, particularly in prairie streams because they contain woody debris which can entangle divers or limit the effectiveness of tactile searches (McAlpine and Sollows 2014). Woody debris also poses a challenge when completing excavations to locate buried mussels (McAlpine and Sollows 2014). Prairie streams are hydrologically variability, which makes sampling even more difficult because large portions of the stream may dry during the summer creating issues for access and stream navigation (Dodds et al. 2004). Creating effective landscape models to understand how and why mussels are distributed may require combining traditional sampling with new and innovative approaches.

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 (Hoftyzer et al. 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 informative. This information would allow reintroductions to be informed about where appropriate species are located based on their ability to tolerate certain forms of environmental perturbation. Therefore, the goal of my thesis was to provide information on cross-scale environmental linkages and how these factors influenced mussel distributions. I pursued two objectives to attain this goal. The first objective focuses on improving techniques to detect species in turbid, deep-water environments that are often difficult to sample. The third chapter uses data from the second chapter to build models that evaluate the importance of landscape and in-channel factors to the distribution of several mussel species.

Objectives:

1. Determine the usefulness of side-scan sonar as a tool to locate freshwater mussel beds;
2. Evaluate environmental factors at multiple spatial scales that influence mussel distribution and abundance on the Muddy and Clear Boggy rivers.

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CHAPTER II

EVALUATING THE USE OF SIDE-SCAN SONAR FOR DETECTING FRESHWATER MUSSEL BEDS IN TURBID RIVER ENVIRONMENTS

INTRODUCTION

Freshwater mussels are an ecologically important component of lotic ecosystems. In many stream systems, mussels make up a large portion of the biomass and provide important ecosystem functions (Strayer et al. 1999, Vaughn and Hakenkamp 2001). Freshwater mussels influence ecosystem processes across a range of trophic states through particle processing (i.e., filter feeding) and release of nutrients from captured suspended matter in the form of pseudofeces (Vaughn and Hakenkamp 2001, Vaughn et al. 2004, Howard and Cuffey 2006). Vaughn et al. (2004) found a linear response among mussel biomass and particle processing and nutrient release from pseudofeces. The authors also found these relationships hold when mussels occurred at low densities. Freshwater mussels are a valuable food source to many terrestrial (Toweill 1974, Tyrrell and Hornbach 1998) and aquatic species (Tiemann et al. 2011). Further, freshwater mussels also possess several characteristics that make them sensitive indicators of aquatic ecosystems: they are long lived, relatively sessile, and sensitive to changing water quality, habitat, and fish communities (Neves 1993, Naimo 1995).

A major impediment to the conservation and management of freshwater mussel populations is a general lack of knowledge of their distributions (National Strategy for the Conservation of Native Freshwater Mussels 1998). Knowing where mussel populations are located is an important first step in identifying mechanisms that influence distributions, providing follow-up monitoring to populations, and protecting these areas when necessary. Identifying the location of freshwater mussel beds is challenging and resource intensive (labor and time spent in the field). Traditional sampling techniques involve tactically searching the stream bottom to locate mussels. In clear-water streams, visual searches can be completed using either snorkeling or diving (Miller and Payne 1993, Beasley and Roberts 1996). However, both of these methods are time consuming and may be difficult or impossible to perform over entire river systems, particularly when rivers are deep and turbid.

Side-scan sonar is a technology that is useful for examining features of aquatic systems without the requirement of direct observation. Side-scan sonar works by emitting conical acoustic signals down toward the bottom and across a wide angle, perpendicular to the path of the sensor. These acoustic signals are then reflected back to the transducer by the objects acoustic pulse encounters. The time delay from the initiation of the acoustic pulse and echo is related to the distance between the reflecting object and the transducer. Echo data are relayed to the headunit where it stitches the information from the signal to produce a high-resolution two-dimensional image of the underwater landscape (Fish and Carr 1990).

Uses of side-scan sonar have evolved over time due to technological advances. Side-scan sonar was developed in the 1960’s; however, early use was primarily limited to oceans and large bodies of water because it required a big vessel to pull a very large towfish (with transducer attached) through the water (Newton and Stefanon 1975, Fish and Carr 1990, Edsall et al. 1993, Fish and Carr 2001). Side-scan sonar was traditionally used in large open-water bodies to chart navigational channels and identify debris along the bottom (Newton and Stefanon 1975, Hobbs 1985). In the last decade, side-scan sonar technology has advanced leading to the development of smaller units that are relatively inexpensive (~USD $2000). These new side-scan sonar units are able to operate at high frequencies (455 or 800 kHz) and produce high-resolution images (< 10-cm per pixel). With the recent decrease in size and cost, side-scan sonar technology has become more readily available and applicable to inland aquatic systems. With the recent decrease in size and cost, side-scan sonar technology has become more readily available and applicable to inland aquatic systems. Moreover, side-scan sonar has become useful in relatively shallow-water (< 10 m) systems including rivers and streams. Recent applications include in-channel substrate and woody-debris mapping (Kaeser and Litts, 2008, Kaeser and Litts, 2010, Kaeser et al. 2012), and suggest the technology may have other applications in river and turbid aquatic systems (i.e., locating freshwater mussels). The objectives of this study were to 1) develop a series of reference images of freshwater mussels clustered in different substrates to assist in identify mussels from sidescan images, and 2) assess the usefulness of side-scan sonar for locating freshwater mussels under different stream-habitat conditions.

METHODS

Study area

Side-scan sonar images were captured on portions of Lake McMurty and over a 32-km reach of the Muddy Boggy River (Fig. 2.1). Lake McMurtry is a 1,155-acre eutrophic reservoir located in Noble County, Oklahoma, USA. Lake McMurtry was impounded for flood control, and is used for water supply and 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). 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 from 7.9-26.4 m/km (Pigg 1977). The study reach was selected because it is known to currently support freshwater mussel beds (Powers, Unpublished data) and includes several deep pools (> 2 m), 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 contained ideal habitat for illustrating the use of this tool because physicochemical characteristics make traditional freshwater mussel

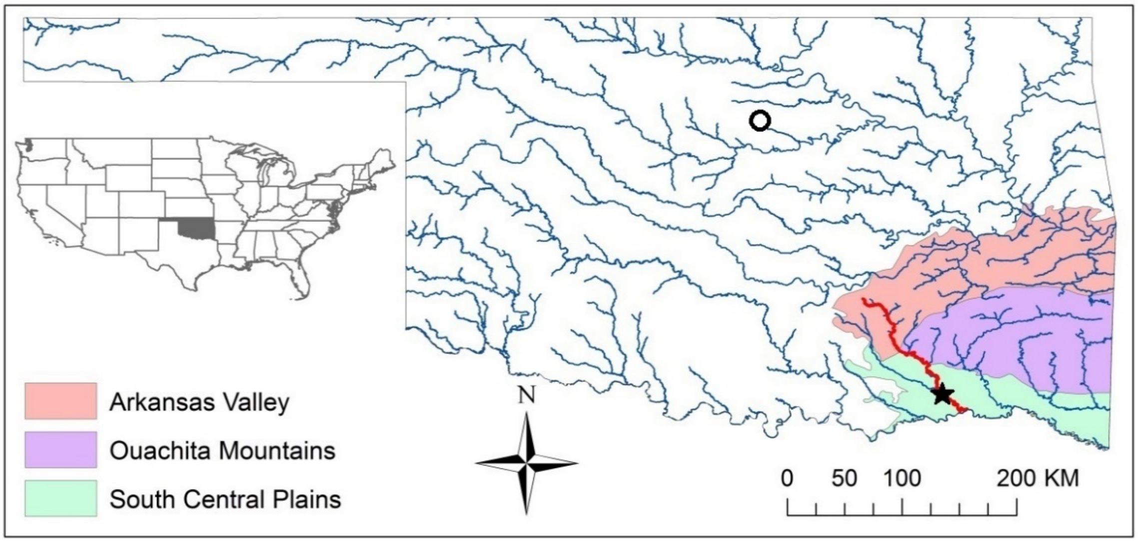

Figure 2.1 Lake McMurtry (open circle) where reference images of placed mussel shells were developed using side-scan sonar and the Muddy Boggy River where the 32-km mussel-bed survey was conducted with side-scan sonar.

sampling difficult. The river carries high suspended sediment loads even during base-flow conditions and has an abundance of instream woody debris.

Development of reference images

I developed a series of reference images using a side-scan sonar system (Humminbird® 1198c SI system, Eufaula, AL, USA) by scanning areas of a reservoir with and without freshwater mussel shells (Lake McMurtry, Stillwater, Oklahoma, USA, Fig. 2.1). I selected several 9-m^2 areas dominated by (estimated visually, the mean percentage and particle diameter in parentheses): silt (90%, < 0.1 mm), sand (90%, 0.1-2 mm), gravel (85%, 2-50 mm), and cobble (85%, 50–250 mm), and scanned each area multiple times to capture images with and without mussel shells present. Snorkel surveys were completed prior to side-scan sonar surveys to check for mussel populations prior to sampling. 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. Water depths within the 9-m^2 area ranged 0.8-1.2 m. Next, I placed 50 mussel (shells matching right and left valve were bound together but did not contain living tissue) of multiple species and sizes throughout the selected 9-m^2 area (Table 2.1). 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 (Allen and Vaughn 2009). Several side-scan sonar passes were then completed using the same techniques with the mussel shells in place. I examined the characteristics of the reflected properties of these images looking for commonalities in the images to apply to unknown areas. Potential mussel beds were determined based on specific criteria: matching pixel size in the map area, comparable pixel size of mussel cluster reflectance, evaluation of longitudinal depth continuum to identify channel units and substrate composition, matching habitat reflective characteristics to reference images, and inclusion of similar reluctance properties within homogenous habitats.

Side-scan sonar imaging and processing

Side-scan sonar was used during base-flow conditions in July 2012 and elevated discharge in May 2013 to capture images of potential mussel beds. The surveys coincided

Table 2.1 Mussel species and mean length and width (mm, range in parentheses) of shells used for reference images. If no range is provided, only one mussel was included in the images.

Species		Length	Width
Amblema plicata	Threeridge	194.89 (120.66-225.55)	71.04 (55.40-76.89)
Fusconaia flava	Wabash pigtoe	77.14 (74.35-79.93)	41.81 (41.49-42.14)
Lampsilis cardium	Plain pocketbook	89.19 (78.82-99.43)	48.10 (43.01-56.31)
Lampsilis teres	Yellow sandshell	96.62 (83.00-110.19)	38.47 (32.62-43.65)
Leptodea fragilis	Fragile papershell	107.24 (90.84-121.59)	36.82 (29.28-42.5)
Megalonaias nervosa	Washboard	169.24 (122.68-204.91)	58.06 (47.01-66.89)
Obliquaria reflexa	Threehorn wartyback	64.39 (63.84-65.43)	38.41 (37.03-40.33)
Potamilis purpuratus	Bleufer	130.72 (95.17-149.84)	56.42 (43.06-66.02)
Quadrula quadrula	Mapleleaf	70.40	38.34
Tritogonia verrucosa	Pistolgrip	98.92	27.77

with the freshwater mussel brooding and feeding activities (March through August) when mussels were more likely to be at the substrate surface. The two different time periods also help to capture different mussel species as not all species will breed at the same time (tachytictic; breeding occurs in the spring and glochidia are released during the summer, bradytictic; breeding occurs in the summer and glochidia are released the following spring. Side-scan surveys were completed in 1-2 d so discharge conditions would be relatively constant on each scanning day.

The side-scan sonar unit was set up to reduce image distortion and capture as much detail as possible in the images. Side-scan surveys were conducted with the side-scan unit mounted on the front of a canoe with the transducer to prevent the wake from causing image distortion (Kaser and Litts 2010). A 3.5 hp outboard motor was used to power the canoe at a relatively constant speed of approximately 6.5 kph to capture consistent sonar imagery. Prior to imagery capture, I compared multiple scanning frequencies: low (455 kHz- side-scan beam) and high (800 kHz- side-scan beam). The optimal scanning frequency is a balance between capturing the entire stream channel bottom and obtaining high-quality image resolution. For the purposes of this study, which required locating small mussels, I used high-frequency scans (800 kHz) to evaluate the ability of side-scan sonar to identify mussel locations (Fig. 2.2). During side-scan sonar surveys, all images were captured from approximately a mid-channel position. Captured side-scan images were recorded as video files and the corresponding Global Positioning System (GPS) coordinates were recorded to a secure digital high capacity (SDHC) memory card in the side-scan headunit for post-processing.

Side-scan images were imported into Dr. Depth® software (DrDepth, Göteborg, Sweden) and processed into a complete static, geo-referenced image mosaic. Processing the images was required as the raw images were not compatible with geographic information system (GIS). Original side-scan 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 were selected to allow the image to join within the mosaic using slant-range correction to ensure geo-referencing was correct for both side images. Mosaic settings for

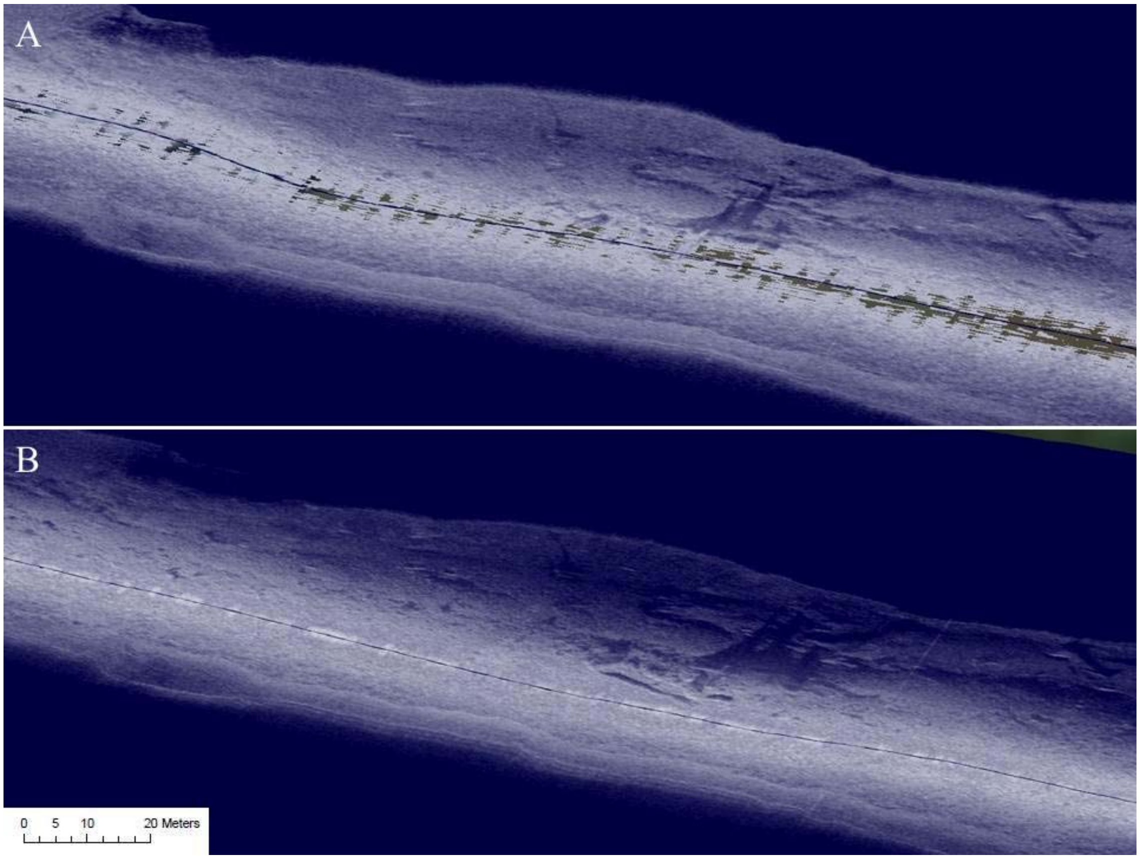

Figure 2.2 Side-scan images of a selected area using two different frequencies for image capture. A) image captured at 455 kHz frequency and B) image captured at 800 kHz frequency.

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 set within the mosaic tool, it was converted to a map image and saved as a KML (.kml) file. Map images were imported into ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA), georeferenced to aerial photographs and converted to a grid file for map-image evaluation in ArcMap (Hook 2011).

Map images were imported into ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA). The 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.

Field validation

Using the reference images as a guide, I determined putative mussel-bed locations in the Muddy Boggy River from the side-scan imagery. I identified 94 areas within the images to be potential clusters of mussels. Validation sites were located using GPS coordinates of the upstream and downstream locations of the possible bed location. A 5-m buffer was added to the perimeter of the site to account for GPS error and ensure complete sampling. 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. I recorded the presence of any mussel shells in addition to approximate densities within the area examined. I 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 parameters

Habitat characteristics were measured at each of the 17 sites chosen for field validation to determine if side-scan sonar more accurately identified mussel beds in some habitats than others. I haphazardly measured depth (1.0 cm) at 3-6 points and recorded temperature (ºC) at each site. The number of depth points measured depended on the size of the area sampled and the extent of the mussel bed. Dominate 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). I measured average water-column velocity at 0.6 from the water's surface (if depth < 0.8 m) or averaged measurements from 0.2 and 0.8 from the surface (when depth ≥ 0.8 m) using an electromagnetic flow meter (Marsh McBirney, Loveland CO, USA). Mean depth and velocity and the coefficient of variation were calculated from subsamples taken at each site. Bankfull width (0.10 m) and bankfull depth (0.10 m) were measured one time at each site following methods of Gordon (2004).

Statistical analyses

I developed a logistic regression model to determine what habitat factors positively related with accurate mussel bed detections from the side-scan sonar images. First, explanatory variables were evaluated for multicollinearity using Spearman's rank correlation coefficients to exclude highly correlated variables from the final model ($|r| \geq 0.28$, Graham 2003). To prevent bias when examining multicollinear variables, I selected a subset of variables for model building that I hypothesized would have the most influence on detecting mussels. Additionally, I excluded temperature and velocity because there was little variation in the measurements across study sites. The final set of variables was used to create a logistic regression model using forced entry (forced logistic regression, Colombet et al. 2001). If the model was significant ($\alpha \leq 0.05$), standardized coefficients were calculated to determine the importance of the explanatory variables in the model. The interaction between depth and sinuosity was fit to an additional model to assess if the influence of depth might depend on stream sinuosity. I completed diagnostic procedures using residual plots (Pearson and Deviance) to identify observations that were not explained well by the model. I also examined influence statistics (DFBETA, DIFDEV, and DIFCHISQ) to measure changes in the coefficients if an observation was deleted (Allison 1999). These statistics allowed the influence of individual observations on the model outcome to be examined to prevent undue influence from limited observations. The Hosmer-Lemeshow test is often used to evaluate model fit via logistic regression but is not appropriate for very large or small data sets. Therefore, I evaluated model fit using the *c*-statistic (values range from 0.5-1.0) where values near 0.5 suggest poor model fit and values near 1.0 indicates the model classifies cases very well (Field and Miles 2010). Analyses were completed using Statistical Analysis Systems (proc logistic, SAS Institute, Cary, NC, USA).

RESULTS

Reference imagery

Using the captured images of mussel shells within different substrate types, I was able to create reference images based on the reflectance characteristics (signal reflected off objects at varying strengths apparent in image captured) of the shells. Mussel shells placed in coarse substrates (i.e., pebble and cobble) and fine silt were nearly impossible to identify from the surroundings substrates (Fig. 2.3 and 2.4); however, I was able to easily distinguish mussel shells placed within sand and clay. Mussel shells were clearly visible as a cluster of white dots scattered within the fine substrate (Fig. 2.3 and 2.4). The hardness and size of the mussel shells compared to the surrounding substrate contributed to relatively clear images of the mussels. The increased hardness of the mussel shells compared to soft and fine substrates allowed more reflectance of the sound pulse, providing better contrast relative to soft substrates. This pattern was consistent even at increased horizontal distances (Fig. 2.4).

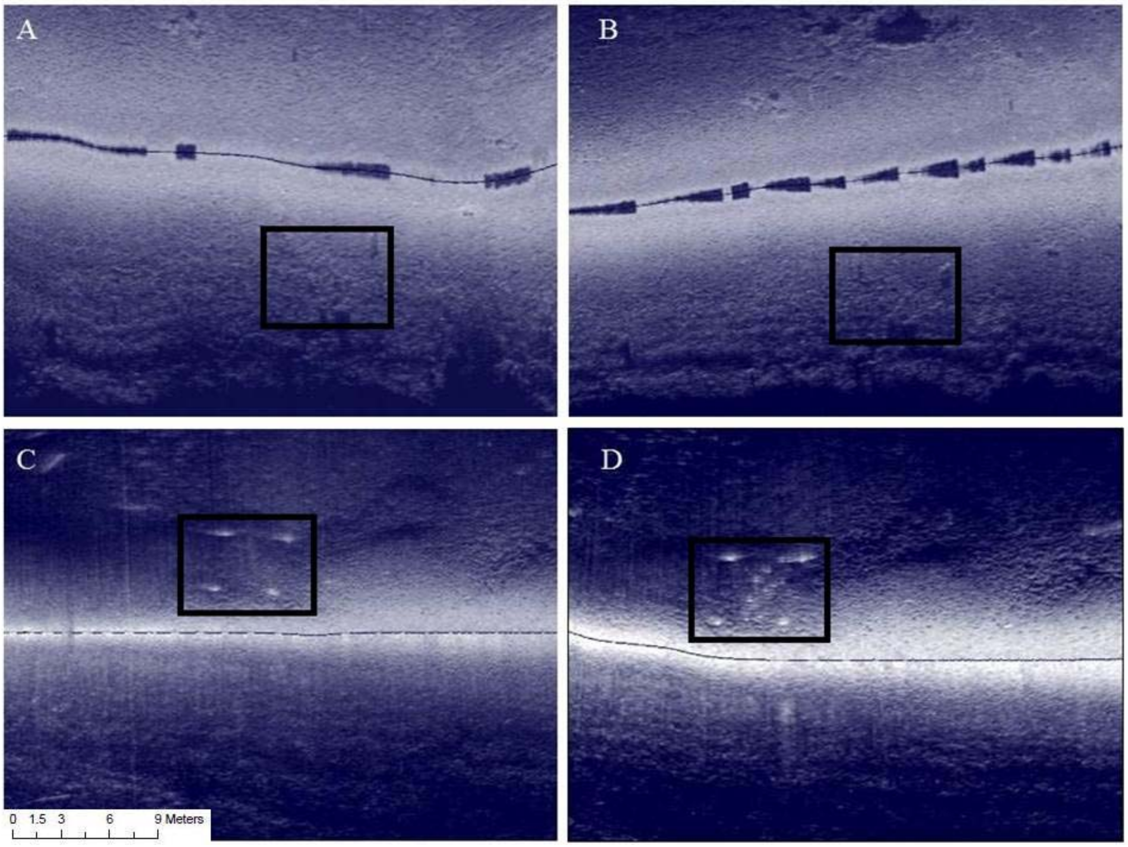

Figure 2.3 Side-scan images including 9-m^2 areas of Lake McMurtry, Oklahoma containing: A) coarse substrate with no mussel shells, B) coarse substrate with mussel shells, C) fine substrate with no mussel shells, and D) fine substrate with mussel shells. The four white images in Panel C and D are reflectance from T bars outlining the sample area.

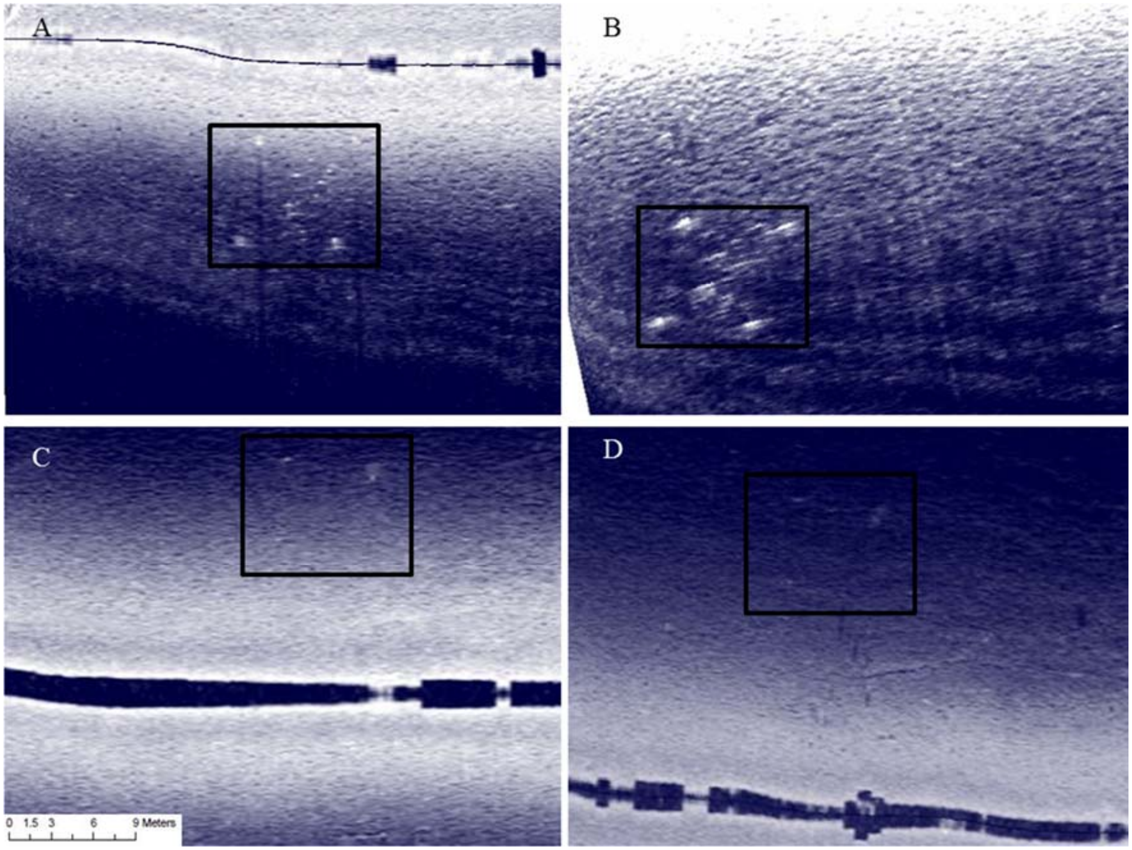

Figure 2.4 Side-scan images including 9-m^2 areas of Lake McMurtry, Oklahoma containing: A) fine substrate with mussel shells, captured at 5 m, B) fine substrate with mussel shells, captured at 10 m, C) coarse substrate with mussel shells, captured at 5 m, and D) coarse substrate with mussel shells, captured at 10 m. The four white images in corners of the selected image are reflectance from T bars outlining the sample area.

Side-scan sonar mapping

Captured side-scan sonar survey imagery of the two sampling periods (July 2012 and May 2013) revealed that images captured at elevated discharges were more complete and provided more image detail than images captured at base-flows. Images captured at base-flow conditions often lacked complete bank-to-bank coverage and had gaps in image capture (e.g., riffles and runs with extreme low flow). Survey images captured at elevated discharges provided a more complete picture of the stream bed and allowed for better identification of potential mussel beds. Both survey images were used to identify potential mussel beds, however, the images recorded during May were more likely to contain areas that had similar reflectance properties to that of my mussel reference images.

Field validation

Field validations demonstrated that side-scan sonar is effective for locating mussels. Field validations revealed approximately 60% (10 of 17) of sites where sonar data suggested mussels were present were confirmed to be actual mussel beds based on my criteria. However, four additional locations (approximately 25%) had living mussels, mussel shells, or both present but did not fit my definition of a bed. Therefore, side-scan sonar was 80% affective at locating mussels (i.e., 14 out of 17 sites where side-scan sonar indicated mussel presence were verified to contain mussels).

Habitat associated with mussel-bed presence

Spearman's rank correlation coefficients indicated several habitat variables (58% of all possibilities) were multicollinear ($|r| \geq 0.28$, Table 2.2). 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 I 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

Table 2.2 Matrix of relative *r*-values for Spearman's rank correlation coefficient of mussel bed habitat variables. Values of $|r| \geq 0.28$ were considered multicollinear (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*

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 sinuosity. Residual plots and influence statistics indicated that one observation had a major influence on the regression parameters (deviance value was 6.95). I 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 depth and sinuosity interaction was not significant ($P = 0.11$), and therefore the interaction term was not included in the final model.

My final logistic regression model indicated that depth was significantly related to my ability to detect mussels using side-scan sonar (Table 2.3). My ability to accurately identify potential mussel beds was greatest at water depths of approximately 1 - 2 m (83%, 10 out of 12 sites confirmed as mussel beds), whereas my ability to accurately identify potential mussel beds decreased in the deepest areas sampled (2 - 3.4 m, 45%, 5 out of 11 sites confirmed as mussel beds). Model fit was considered very good (*c*-statistic= 0.91).

DISCUSSION

I have shown that side-scan sonar can be a useful preliminary tool for locating freshwater mussels over a broad area under environmental conditions where traditional sampling may be prohibited over long distances. Approximately 60% of the sites where side-scan images suggested mussels were present had mussels beds whereas about 80% of the sites had mussel shells. This is one of the first studies that I am aware of that used an inexpensive side-scan sonar system in a river to locate freshwater mussel beds, so it is difficult to compare my results directly to existing studies. My results are similar to a study that used a large and more expensive side-scan sonar unit with a towfish to accurately map (~80%) zebra mussel *Dreissena polymorpha* coverage on substrate in Lake Erie (Haltuch et al. 2000). Although side-scan sonar is a useful tool, some refinement would likely improve detection. Mussel detection diminished at water depths

Table 2.3 Values of beta, standard error, odds ratio and confidence intervals for the logistic regression model relating habitat conditions with the presence of mussel beds as observed by side-scan sonar. Significant variables ($\alpha \leq 0.05$) are indicated by asterisks.

			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

≥ 2 m. This may be a result of the angle at which the side-scan sonar signal is reflected from the mussel shells due to bottom slope. 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. Some of my error in identification of mussel beds may have been the result of sampling 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). The quality of my reference images taken in areas of silt substrates were also poor. False positives associated with deeper pools may also have contained isolated patches of coarse substrates surrounded by fines and thus appeared as mussel aggregations. My reference images, developed under relatively homogenous substrate conditions in a reservoir, suggested substrate was major factor limiting the use of side-scan sonar for locating mussels; however, W:D ratios (highly correlated with dominant substrate) was not a good predictor of mussel presence via evaluation side-scan sonar images. Increased heterogeneity within the channel may be one reason why most of the habitat factors were more difficult to determine with my logistic regression model. For example, increasing the resolution of habitat mapping by capturing substrate at each 1-m area scanned rather than dominant substrate across a channel unit would likely provide more insight. Other physical factors that we did not measure may also be important determinants of useful side-scan sonar images (e.g., woody debris, microhabitat substrate mapping, suspended sediment).

Side-scan sonar can help managers safely locate freshwater mussels in areas that may be too difficult or dangerous 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 selected for mussel sampling because they are easier to sample than 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). Side-scan sonar is a helpful tool that allows 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 gain information on assemblage structure and population dynamics.

Using a tool to target intensive sampling locations is important when directing limited resources. A two-person team can survey a 32-km reach with side-scan 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 2005). Although time spent in the field using side-scan sonar is substantially less when compared to traditional sampling, processing the sonar data for a reach of this size takes about 40 to 60 h (~1.5 hours per km); however, user experience can substantially decrease time. These times vary depending on habitat conditions and the speed traveled when sonar data are collected. In addition, side-scan 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) that may be helpful when evaluating mussel-bed distributions. Quickly identifying underwater habitats associated with a mussels allows less time spent in the field and offers insight into potential environmental influences.

Side-scan sonar provides an inexpensive and effective method for locating freshwater mussels, though its application is limited. The side-scan sonar unit I used in this study cost approximately US $2000, substantially less when compared to other side-scan 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). My ability to identify freshwater mussel aggregations using side-scan sonar was good but limited to moderate depths (1-2 m). Incorporating a towfish could potentially improve detections in deeper water. Several resources are available to describe how transducers can be modified into a towfish (e.g., http://forums.sideimagingsoft.com, http://bb.sideimageforums.com). Additionally, attaching the transducer to a longer pole may allow for better image quality by reducing water depth between the transducer and the bottom. Successful identification of mussel-bed locations within the sonar images was limited to areas of fine substrates (e.g., sand and clay). My findings agree with Haltuch et al. (2000) that side-scan sonar is most useful in distinguishing features in fine-substrate environments. The time of year when sampling can be conducted and the 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 of time ineffective for locating mussel beds. Sampling during the freshwater mussel reproductive cycle provides the best opportunity to capture sonar images of a mussel bed as many adult mussels will be found at the substrate surface. There are two reproductive periods, one early season (tachytictic: late spring, early summer) and one late season (bradytictic: late summer) (Graf and Foighil 2000, Galbraith and Vaughn 2009). Because sampling during elevated-discharge conditions ensures adequate image capture of the entire channel in a single survey and provides ideal navigation conditions (Kaeser and Litts 2010, Kaeser et al. 2012), I suggest sampling during the early reproductive season provides the greatest chance of discovering mussels in regions with elevated spring discharge. However, the usefulness obviously depends on what reproductive period is used by the majority of species within the region. Side-scan sonar can still be used during low-flow periods but I found navigation during these periods difficult and it resulted in an increase in image distortion in shallow water and required multiple scanned images in locations where the side-scan sonar unit was turned off to navigate shallow hazards.

Taking the proper steps to refine sonar image capture quality will improve the clarity and reliability of side-scan 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 low-frequency imaging to capture bank to bank images but this would reduce the resolution of the data. 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 side-scan sonar surveys would also allow for cross comparison among recorded sonar images. Comparisons among multiple side-scan images can help validate potential mussel-bed locations if the same mussel bed is present in multiple images even when habitat conditions have changed.

I provided initial reference images for other investigators; however, more images would be helpful under controlled environmental conditions. In particular, developing reference images to distinguish shell characteristics in more heterogeneous habitats would be helpful. I can clearly define shells in homogenous fine substrates but my commission errors likely result from some coarse substrates being located at those sites. One way to improve detections would be to scan during winter when mussels are beneath the substrates and then re-scan when mussels should 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 side-scan sonar surveys of a study area over a short period of time would likely improve detection accuracy. I anticipate the refinements made by sampling multiple passes over multiple seasons will increase the accuracy of detecting mussels in turbid environments making side-scan sonar more broadly applicable to freshwater environments. However, the reference images provided in the current study can be used to examine mussel beds in other aquatic environments if species have similar shells and the riverbed is dominated by similar substrate conditions. Additional reference images from rivers with differing morphologies or containing a different assemblage would also be beneficial.

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CHAPTER III

THE INFLUENCE OF BIOTIC AND ABIOTIC FACTORS ON THE DISTRIBUTION AND ABUNDANCE OF FRESHWATER MUSSELS

INTRODUCTION

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., release 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 (1998) identified ten concerns related to freshwater mussel conservation. Nearly 20 years later, we still lack information on the habitat needs of many species, how to better choose relocation sites for restoration programs, and the population dynamics and distributions of many mussels (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 in population sizes of host fish (Newton et al. 2008, Downing et al. 2010). Habitat degradation, particularly in riparian habitats, is a leading cause of mussel declines (Downing et al. 2010). 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 affects 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 2006). To further exacerbate the situation, climate change is expected to alter precipitation and temperature patterns (Girvetz et al. 2009), which 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 now better understand 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.

Understanding the influence of habitat on mussel distribution and abundance have 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 focused on the importance of microhabitat features (e.g., water depth, Strayer 1981; velocity, Layzer and Madison 2006), but investigators disagreed about the importance of these features (Strayer and Ralley 1993, Brown et al. 2010). Macrohabitat variables were significant in some studies aimed at juvenile distributions (e.g., shear stress, Strayer et al. 1999, Layzer and Madison 2006, Morales et al. 2006; current velocity, Layzer and Madison 2006), but often were not good predictors of adult mussel distributions (Di Maio and Corkum 1995, Hardison and Layzer 2001, Layzer and Madison 2006, Allen and Vaughn 2010). At the reach (often 40 times wetted width) or stream segment (tributary to tributary confluence) scales, hydraulic factors (Steuer et al. 2008), sinuosity (McRae et al. 2004), and habitat degradation (Box and Mossa 1999) correlate with mussel abundance. More recent studies have found 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). At the landscape scale, mussel distributions correlate with 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). An excellent exception is Daniel and Brown (2013) who incorporates various abiotic and biotic factors at multiple scales to predict mussel distributions. Effective conservation and restoration strategies would benefit from an examination of factors at multiple spatial scales.

Improving our ability to identify suitable mussel habitat for reintroductions requires an understanding of the interactions that occur *between* spatial scales. Interactions operate among ultimate, intermediate, and proximate factors (Stevenson 1997) and these relationships may dictate the perceived importance of spatial scale. For example, in regions of highly impermeable soils (i.e., an ultimate factor), increased runoff to streams can increase instream sediment (i.e., a proximate factor) thereby reducing smallmouth bass (*Micropterus dolomieu*) abundance (Brewer et al. 2007). Depending on the scale of investigation, the perceived relative importance of any variable may change. At a fine scale, substrate may be assumed important to mussel presence; however, when viewed at a coarse scale, we may learn that the association with the substrate was determined by regional lithology or soils (ultimate factors). Excess sediment is often implicated as a significant factor leading to truncated distributions and abundances of freshwater mussels (Layzer and Madison 2006) and it is assumed to be related to land-use change (Box and Mossa 1999), but rarely are the two factors 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. Understanding cross-scale linkages will enhance the ability of managers to identify areas likely to be successful reintroduction sites.

Improving or restoring freshwater mussel populations requires an understanding of habitat needs and environmental factors that are related to species persistence. Captive breeding is a common strategy used for improving population numbers (Thomas et al. 2010, Carey et al. 2015). For example, the Peoria Tribe of Oklahoma propagates freshwater mussels for reintroduction into the Neosho River (Shannon Brewer, personal communication). Reintroduction of mussels is often accomplished by choosing what is perceived to be suitable habitat (Cope and Waller 1995, Peck et al. 2007) and often is based on qualitative criteria (Cope and Waller 1995, Peck et al. 2007). Reintroduction failures are common (> 50% of reintroductions evaluated failed in the U.S.; Cope and Waller 1995, Peck et al. 2007) because we lack a real understanding of the mechanisms related to the initial population failure (Hoftyzer et al. 2008). Carey et al. (2015) indicate that successful mussel reintroductions will only be realized when we take a broader approach in identifying relocation sites and evaluate both biotic and abiotic influences on mussels. 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. The objective of this chapter was to evaluate the importance of environmental factors at multiple spatial scales in shaping the distribution of mussel beds and individual species and mussel abundance. My general approach was to develop models that predicted mussel-bed locations and presence and densities of four individual species: bleufer *Potamilis purpuratus,* fragile papershell *Leptodea fragilis,* pimpleback *Quadrula pustulosa,* Wabash pigtoe *Fusconaia flava*. These species were chosen because they occur throughout both the Muddy Boggy and Clear Boggy rivers and each has specific traits making them suited to specific environments.

METHODS

Study area

A detailed description of the study area was provided in Chapter 2. Briefly, the Muddy and Clear Boggy rivers are large, turbid tributaries of the Red River, Oklahoma (Fig. 3.1). Mean annual discharge of the Muddy Boggy is 25.2 m^3/s and the Clear Boggy is 13.5 m^3/s. The rivers traverse five ecoregions that transition from the rugged headwaters to the wide valley at the confluence. Land use in the catchments are predominantly agriculture and pasture, with the greatest amount of agriculture (73%) occurring in the Clear Boggy catchment (Table 3.1). Width-to-depth ratios typically increase in a downstream direction and the Muddy Boggy River is much wider and deeper than the Clear Boggy River. The rivers represent typical riffle-pool morphologies and dominant substrate shifts from coarse material to sand from the headwaters to the Red River.

Identifying species' presence

Freshwater mussel presence and densities were determined using a two-stage sampling approach. The first stage was completed in summer 2011 to identify coarse-scale longitudinal distributions on the Muddy and Clear Boggy rivers (Fig. 3.1). Each river was divided into 10, 32-km segments and six segments on each river were haphazardly selected (based on access). I 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, I 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

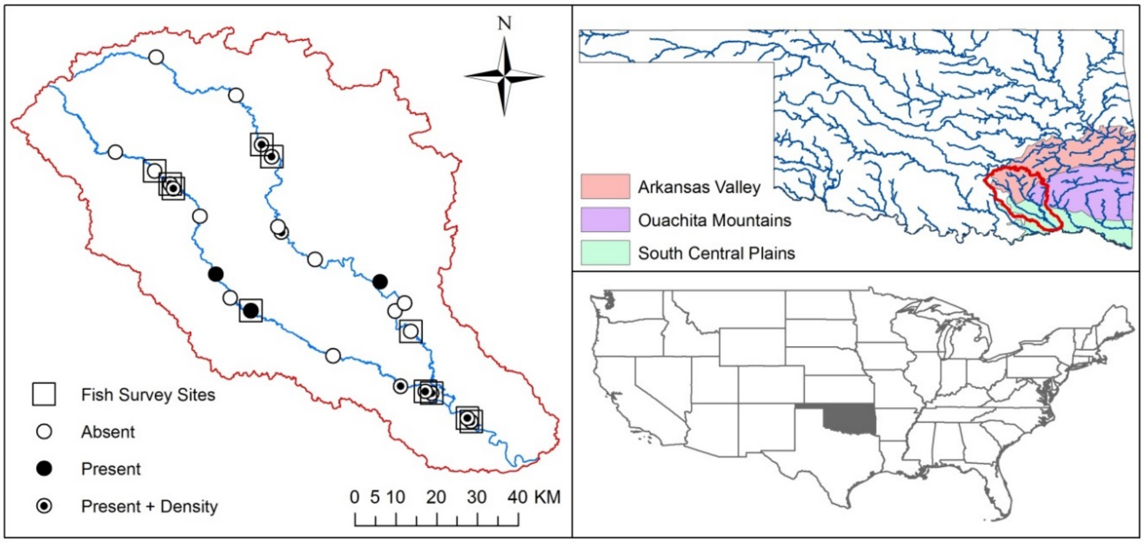

Figure 3.1 Locations of sample sites on the Muddy Boggy and Clear Boggy rivers. The Muddy Boggy River is the eastern river and begins at the confluence of the Red River. All sites on the Muddy Boggy River are numbered from downstream to upstream as MB1 – MB13. The Clear Boggy River is the western river, beginning above the confluence with the Muddy Boggy River, and all sites are numbered from downstream to upstream as CB1 – CB12.

Table 3.1 Descriptive statistics (mean and range) of environmental variables used in competing hypotheses.

Variable	Abbreviation	Muddy Boggy River	Clear Boggy River
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 (m)	Rip	138.95 (76.00-196.20)	113.67 (43.40-206.40)
Agriculture/pasture (%)	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 (km^2)	Drain	2193.30 (119.61-5860.83)	1443.64 (303.94-2588.89)

occurred within 2 m of another mussel. 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 and identifying rare species and juveniles. Systematic sampling in summer 2012 occurred at six of the previous sites from 2011 sampling (MB1, MB8, MB11, CB1, CB3, and CB10) and four new sites (MB2, MB10, CB2, and CB9) in summer 2013 (Fig. 3.1). Previous sampling was conducted at the sites to confirm the spatial extent of the mussel beds. I 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). I then systematically sampled 10-20% of the mussel bed depending of 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). 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, I 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.

Deep-water mussel beds

Side-scan sonar (Humminbird® 1198c SI system, Eufaula, AL, USA) was used to locate mussel beds in deep-water habitats (> 2 m average) of a 32-km reach on the downstream portion of the Muddy Boggy River (Powers et al. 2015). I used side-scan sonar reference images to identify potential mussel-bed locations that were later verified via self-contained underwater breathing apparatus (SCUBA) and snorkeling. Sites that met the criteria of a mussel bed were recorded and presence and absence locations were integrated into the analyses of mussel-bed presences. Only deep-water sites with species identified for analyses were included.

Fish sampling

Six fish-sampling sites were longitudinally stratified on each river: three on the Clear Boggy River and three on the Muddy Boggy River (Fig. 3.1). Selected sites were in close proximity to known mussel-beds (identified in 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. I 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 occurred at all six sampling sites. The second phase of sampling was completed in mid to late March 2013 and occurred at five of the six sampling sites. One site (MB3) was not resampled because access was denied on private land. Gill nets, hoop nets, electrofishing, and seining were all used to sample the fish assemblage to account for differences in habitat use by fishes and gear bias via different fish species (Bonar et al. 2009). Gill nets (24-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 fished 6-8 h in deep-water habitats (> 1 m). Tandem hoopnets (series of 3 nets bridled together: 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, USA) were set overnight (~24-hrs) in run habitats (one series upstream and downstream) parallel to the river bank with cod ends positioned upstream. Each hoopnet was baited with 1 kg of ground cheese logs (Boatcycle, Inc., Henderson, TX, USA). Each hoopnet 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 bar mesh) and techniques described by Bonar et al. (2009). I combined seining and backpack electrofishing (60 Hz, pulsed DC with a 10-15% duty cycle and voltage between 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 my sample area or preserved in 10% formalin and later identified in the laboratory.

I developed simple linear regressions to examine the relation between fish-host abundance (independent variable) and mussel-species density (dependent variable) of four mussels. Fish-host data were expanded to include additional sampling sites that were in the same river segment. For example, if fishes were sampled at one site and other sampling sites occurred in the same river segment (tributary to tributary), I assumed that the same fish would occur at other sampling sites in close proximity (within the same river segment). No obvious fragments (e.g., culverts) occurred in these stream segments. Model assumptions for normality were evaluated using the Anderson-Darling test and normal quantile plots. Variables were natural log (X+1) transformed to satisfy assumptions of normality. Statistical analyses were performed using Statistical Analysis Systems (Proc GLM, SAS Institute, Cary, NC, USA).

Habitat variables

Habitat data were collected at multiple spatial scales: 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, I calculated the proportion of each lithology 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 coarse substrates with higher gradients were classified as riffles. Smooth, unbroken flow that often transitioned riffles and pools and had moderate velocities were classified as runs. 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 at each site (Table 3.2). I calculated the catchment area (1 km^2; Drain) draining to each site using ArcMap. I measured the proportion of lithology for each segmentshed using the National Scale Geology layer and ArcMap (NRCS; Table 3.2). Using the Soil Survey Spatial and Tabular data layer (Table 3.2), I was 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). I then measured the proportion of highly erodible land for each segmentshed. Sinuosity 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).

I created a buffer area around each study site to identify the influence of habitat factors at finer 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). I used aerial photographs of the catchment (NAIP; Table 3.2) and clipped this to my selected buffers. I then delineated the clipped buffer area by creating polygons around agriculture and pasture land, forested vegetation, and riparian corridor width and then I calculated proportions within the buffer for each variable.

Table 3.2 Sources and resolution of geospatial data used in 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

Several reach and microhabitat factors were measured at each sampling site. Bank-soil composition 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 3.2). 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. Microhabitat factors were measured at all sampling sites. Substrate composition was visually estimated 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). In areas where only gravel-sized particles or finer occurred (silt 0.059 mm, sand 0.06–1.00 mm, gravel 2 mm; Bovee and Cochnauer 1977), a shovel of substrate was removed, dried, sieved (2 mm and 150 microns), and weighed to determine percentages of each fine substrate group.

Hypotheses Development

I developed *a priori* models (hypotheses) to predict the habitat factors at multiple spatial scales that had the most support for species presence (Table 3.3) and density (Table 3.4) of the bleufer, fragile papershell, pimpleback, and Wabash pigtoe. Fish-host data were not included in the hypotheses because these data were only collected at a subset of sites to better understand the longitudinal changes. Hypotheses were developed based on the existing published literature. Four hypotheses were developed for species presence and species density using habitat factors that were thought to have the greatest influence on each species: drainage area, agriculture and pasture land, riparian vegetation, forest cover, soil, sinuosity, width-to-depth ratios, and substrate. Drainage area is a key factor influencing the longitudinal continuum of aquatic habitat (Strayer 1993, Dodds et al. 2004, Atkinson et al. 2012). Bleufer and fragile papershell 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

Table 3.3 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,	Influence timing and input of fine	McRae et al. (2004), Strayer (2006)

	sinuosity, and – related to HEL	sediments	
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 3.4 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)

(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, Hardison and Layzer 2001, Layzer and Madison 2006, 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 habitats (Gordon 2004, McRae et al. 2004). Thus, I hypothesized straight channels would decrease species presence and abundance due to increased stream bed scour (Gordon 2004, McRae et al. 2004). Substrate preference may also vary among species (Cummings and Mayer 1992, Vanleeuwen and Arruda 2001), with selection potentially influenced by shell morphology. In general, species with smooth shells are hypothesized to use fine substrates, whereas species with shell ornamentation or obese shells are hypothesized to occur in medium to coarse substrates (Watters 1994b). However, many mussel species are considered substrate generalists (Murray and Leonard 1962, Oesch 1984, Howells et al. 1996).

I developed four competing hypotheses to predict the relative importance of habitat factors at various spatial scales on mussel-bed presence (Table 3.5). The four hypotheses focused on the importance of drainage area, proportion of shale lithology, soils, agriculture and pasture land, riparian vegetation, and sinuosity to mussel bed

Table 3.5 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)

presence. I 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). I hypothesized that upstream portions of my study area would be unlikely to support mussel beds because of stream drying during the summer, making it impossible for mussel beds to become established over time (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, Dodds et al. 2004, Layzer and Madison 2006, 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). I hypothesized downstream study sites with high amounts of shale would have fewer mussel beds due to increased erosion of the channel. I also hypothesized that stream segments where shale was the dominate lithology 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). I hypothesized mussel beds were more likely to occur in areas with low erosion potential, because highly erosive conditions increase fine sediment within the channel thereby creating unsuitable mussel habitat (McRae et al. 2004, Strayer 2006). Agriculture land use also alters the amount and timing of water and sediment delivery to streams, which alters natural disturbance regimes and degrades mussel-bed habitats (Box and Mossa 1999, Arbuckle and Downing 2002). I also hypothesized wider riparian corridors would be beneficial to mussel beds because a wider riparian corridor can reduce bank erosion and excess sediment delivery to the channel (Wenger 1999, Sweeney et al. 2004). In addition, I 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 increase 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, I standardized my explanatory variables and performed preliminary diagnostic procedures. 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 appropriate comparisons when the scales may differ. For example, the drainage area of the Muddy Boggy was much greater than the Clear Boggy leading to increased variation in the data set which if not accounted for can lead to misinterpretation of the results.

I completed a Spearman's rank correlation procedure to identify multicollinear variables. Multicollinear variables for my landscape 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, I choose variables that were documented in the literature to have the greatest influence 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. I completed diagnostic procedures using residual plots (Pearson and Deviance Statistics) to identify highly influential points or outliers. Additionally, I checked for significant outliers that might influence the final model parameters using Cook's distance, where values ≥ 1 were considered highly influential.

I developed a generalized linear model (GLM) to determine which combination of habitat factors had the greatest influence on the distribution and density of four species (bleufer, fragile papershell, pimpleback, Wabash pigtoe) and mussel-bed presence in the two rivers. All mussel data included in the models were adult mussels because juveniles were not encountered across all sites (juvenile mussels < 40 mm in length; Wilson et al. 2011). GLM is able to accommodate both continuous and categorical variables and allows for the analysis of non-normal data. Because the dependent variable for my presence models was binary (presence/absence), I used a binomial distribution with a logit link function. I used a negative binomial distribution for models predicting densities (count data) because my data were overdispersed (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 I developed (Table 3.3, 3.4, and 3.5) 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 my hypotheses had the most support. Because of the small sample size ($n/K<40$), AICc was used. The values produced from the models were ranked based on AICc differences (Burnham and Anderson 2002). Based on ΔAICc values, values $\Delta< 2$ suggests 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 had minimal support. For the purpose of determining the models with the most support, I selected a Δ_i cutoff of ≤ 2 as I was 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 as 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 increased support in the model (Mazerolle 2004). Higher Akaike weight values indicate a greater influence in the model (Marchetti et al. 2004). The 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. I 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). Models with higher pseudo R^2 values explained a greater amount of variation in the dependent variable. A cutoff of 30% was used to indicate a 'strong' model (Zuur et al. 2009).

RESULTS

I found 42 mussel beds on the Muggy and Clear Boggy rivers that contained a total of twenty species. Species diversity was the greatest downstream and four of the species encountered were rare: fat mucket, *Lampsilis siliquoidea* (CB10), paper pondshell *Utterbackia imbecillis* (MB10), pink papershell, *Potamilis ohiensis* (MB1, MB10), and rock pocketbook, *Arcidens confragosus* (CB2, MB2). Mussel densities were relatively consistent across all sites (5-7 mussels per 1 m^2), except MB8 where densities were low (3 per 1 m^2) and MB2 where densities were relatively high (15 per 1 m^2; Fig. 3.2).

Deep-water mussel beds

Side-scan sonar results were reported in chapter one. Briefly, I identified 10 deep-water sites where mussel beds occured and seven sites where beds were absent. Thus, I added 17 additional locations to my mussel-bed analyses.

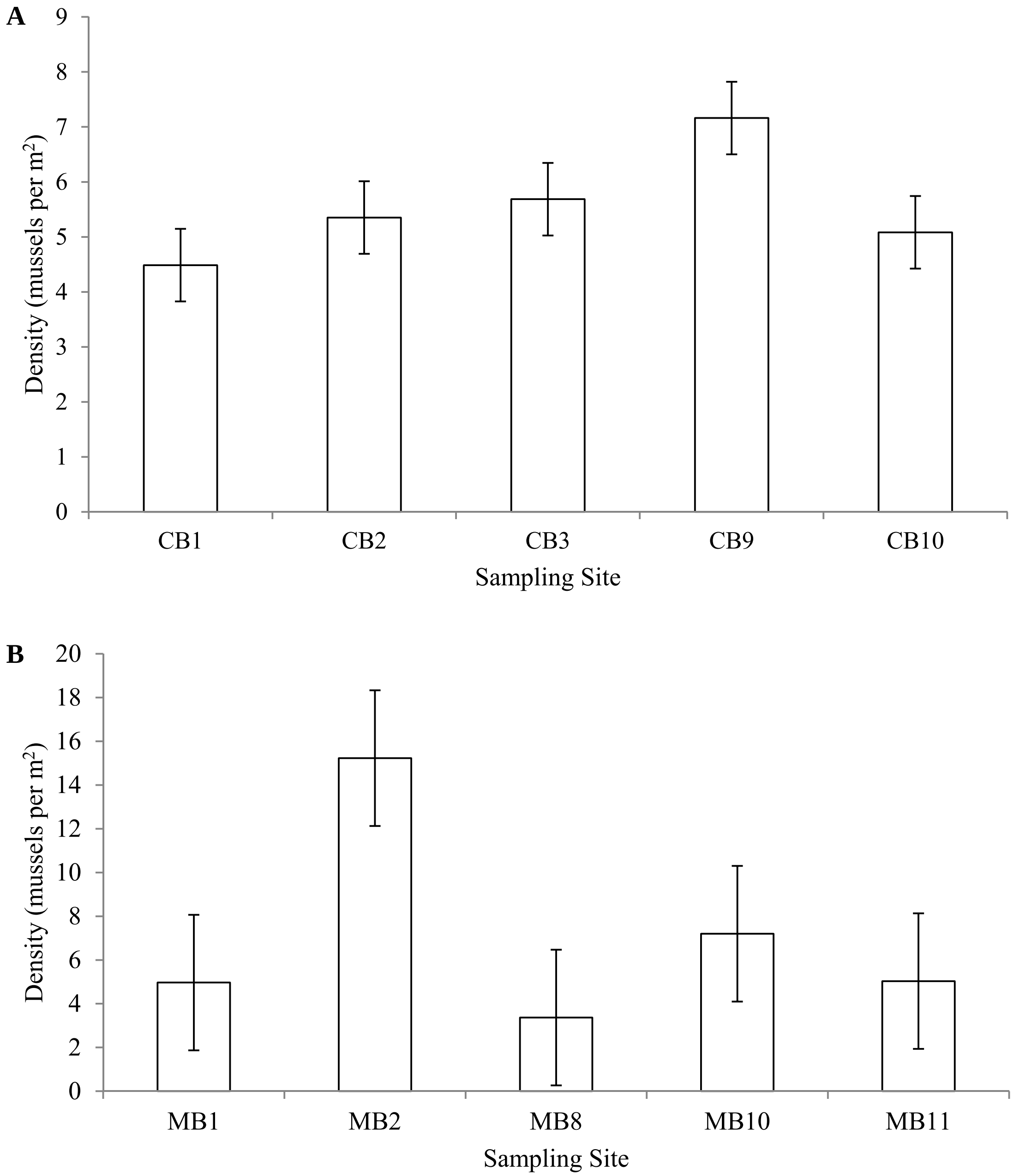

Figure 3.2 Mussel density (per m^2) by site on the Clear Boggy (A) and Muddy Boggy (B) rivers. Error bars represent confidence limits (90%). Study site names were described in Figure 3.1.

Fish assemblage

A total of 2,017 fishes was collected representing 53 species and nine families (Fig. 3.3). Highest species richness occurred at the farthest downstream sampling sites. As I would expect given predictions associated with the river continuum concept (Vannote et al. 1980), fish-host abundances were greatest at the farthest downstream sampling sites and likely relate to increased flow stability (Dodds et al. 2004; Table 3.6).

There was a positive correlation between mussel densities and fish-host abundance (log transformed) for two of the four mussel species. Freshwater drum abundance was positively related to bleufer densities (F= 4.14, P <0.01, R^2= 0.41) and fragile papershell densities (F= 5.01, P<0.01, R^2= 0.46; Fig. 3.4). Fish-host abundance was not significantly related to increases in pimpleback (F= 0.44, P= 0.53, R^2= 0.07) or Wabash pigtoe densities (F= 0.05, P= 0.83, R^2= 0.01; Fig. 3.4).

Diagnostic procedures and correlations

Spearman's rank correlation coefficients for presence data indicated only a few landscape factors (11%, 3 of 28) were multicollinear ($|r| \geq 0.70$, Table 3.7). 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 with riparian corridor width. As expected, proportion of forest and proportion of agriculture and pasture land were significantly negatively correlated. Variables retained for modeling were selected based on their ecological influence on mussel bed presence, species presence, and species densities. I selected agriculture and pasture land use as a variable when considering the effect of excess fine sediments on mussel presence; whereas, I selected riparian corridor when considering the buffering effects of wide riparian corridors on fine sediments.

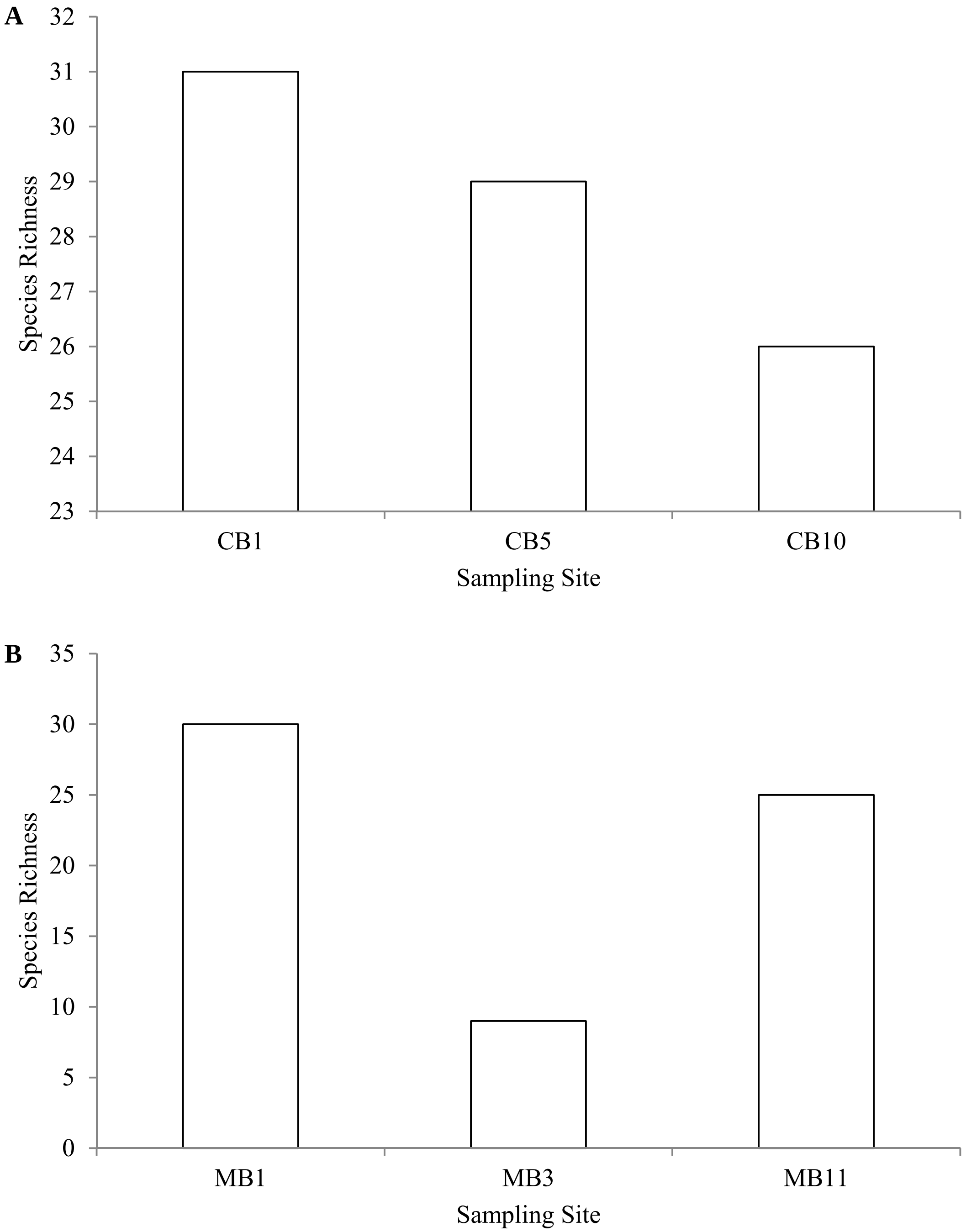

Figure 3.3 Fish species richness at each site on the Clear Boggy (A) and Muddy Boggy (B) rivers. Study site names were described in Figure 3.1.

Table 3.6 Relative abundance (percent of total catch at each site) of fish hosts collected during fish sampling. Number of individuals sampled is provided in parentheses. Site codes were described in Figure 3.1.

Species	Common name	MB1	MB3	MB11	CB1	CB5	CB10
Lepomis macrochirus	bluegill	6% (22)	10% (3)	20% (85)	18% (40)	6% (34)	7% (27)
Etheostoma chlorosomum	bluntnose darter				<1% (1)		
Pimephales notatus	bluntnose minnow	4% (16)		15% (67)	5% (12)	4% (19)	1% (4)
Ictalurus punctatus	channel catfish	3% (12)	7% (2)	1% (5)	5% (11)	4% (20)	13% (52)
Notropis atherinoides	emerald shiner			<1% (1)		<1% (1)	
Pylodictis olivaris	flathead catfish		3% (1)		<1% (1)		1% (3)
Aplodinotus grunniens	freshwater drum	<1% (3)			<1% (1)		
Dorosoma cepedianum	gizzard shad	<1% (1)				<1% (1)	
Moxostoma erythrurum	golden redhorse			<1% (1)			
Notemigonus crysoleucas	golden shiner					1% (3)	
Lepomis cyanellus	green sunfish			9% (37)	4% (10)	<1% (1)	2% (6)
Micropterus salmoides	largemouth bass	1% (2)	3% (1)	1% (4)	3% (6)	<1% (1)	
Percina caprodes	logperch	<1% (1)					
Lepomis megalotis	longear sunfish	1% (2)	32% (10)	3% (11)	9% (20)	<1% (2)	9% (34)
Lepisosteus osseus	longnose gar	3% (11)	3% (1)			2% (13)	1% (4)
Lepomis humilis	orangespotted sunfish	33% (129)		11% (47)	11% (26)	4% (23)	
Notropis stramineus	sand shiner	23% (91)		5% (20)	12% (27)	1% (3)	2% (6)
Lepisosteus platostomus	shortnose gar	1% (2)			<1% (1)		
Percina phoxocephala	slenderhead darter				1% (2)	1% (6)	<1% (1)
Micropterus punctulatus	spotted bass	<1% (1)		<1% (1)	2% (4)		1% (5)
Noturus gyrinus	tadpole madtom	1% (2)		<1% (1)	<1% (1)		1% (3)
Lepomis gulosus	warmouth sunfish	<1% (1)			<1% (1)		
Pomoxis annularis	white crappie		3% (1)	<1% (1)	<1% (1)	1% (3)	
Total		(296)	(19)	(281)	(165)	(130)	(145)

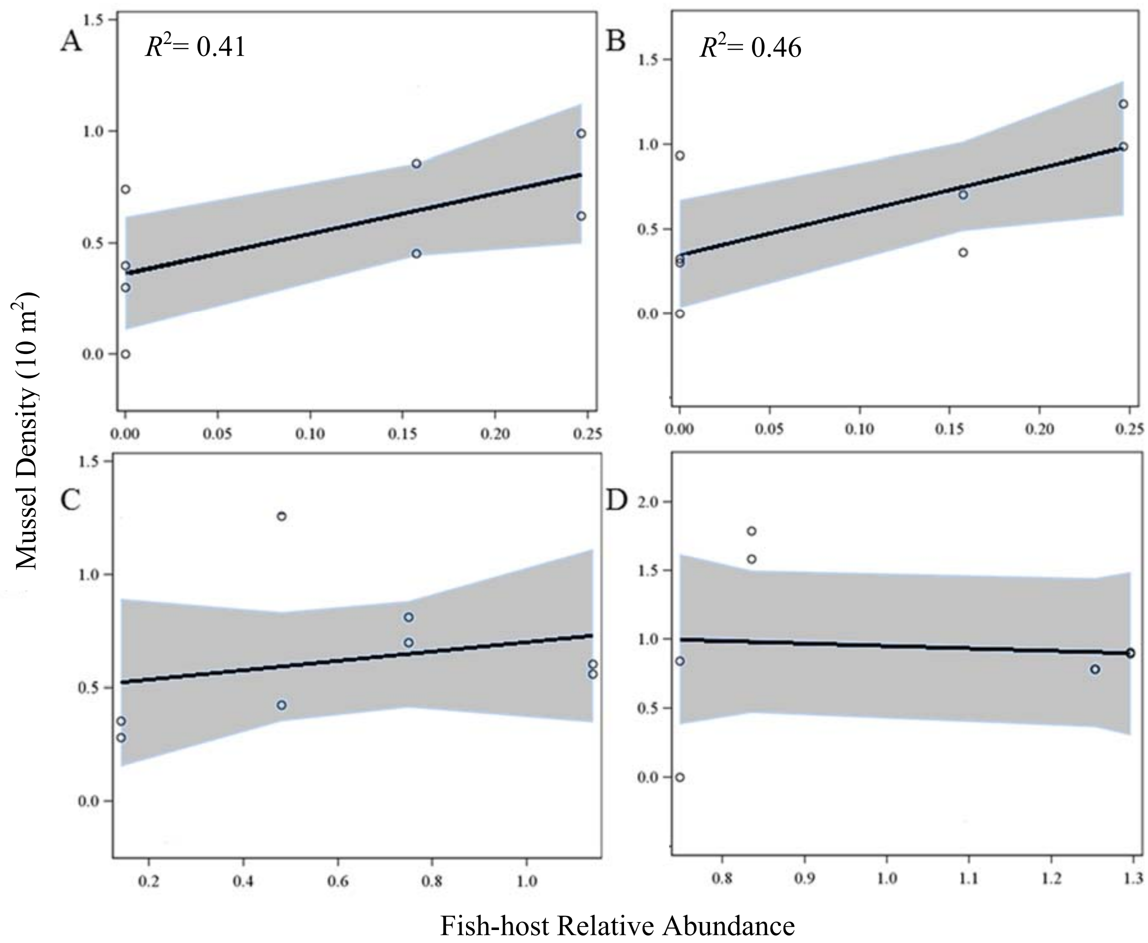

Figure 3.4 Linear regression relating species density (number per 10 m^2) to fish-host relative abundance. Open circles represent data points, solid lines represent fitted regression line, and shaded areas represent confidence limits (90%). Relationships shown are for: A= bleufer B= fragile papershell, C= pimpleback, and D= Wabash pigtoe. R^2 values are provided where the linear relationships were significant ($\alpha \leq 0.10$).

Table 3.7 Matrix of *r*-values for Spearman's rank correlation coefficient related species and mussel-bed presence with abiotic factors. Values of $|r| \geq 0.70$ (indicated by asterisk) are considered multicollinear for landscape analyses. 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

Spearman's rank correlation coefficients for landscape and inchannel variables associated with species density models indicated over a third of the factors (36%, 10 out of 28) were multicollinear ($|r| \geq 0.70$, Table 3.8). Density correlations also indicated highly erodible land, width-to-depth ratios, and shale lithology were highly correlated. Agriculture and pasture land use was multicollinear with all variables except sinuosity. Drainage area was negatively correlated with highly erodible land and agriculture and pasture 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 and none were found.

Models predicting species presence

Results from the AICc model ranking indicated several variables were related to the presence of multiple species. Drainage area was considered 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 portion of the rivers, whereas one species, Wabash pigtoe, occurred most often in upstream reaches. Wider riparian corridors ($\bar{x}$= 123.6 m) were positively related to fragile papershell presence, whereas Wabash pigtoe was more tolerant of narrow riparian areas ($\bar{x}$= 116 m). Riparian corridor width often co-occurred with drainage area or agriculture and pasture land in supporting models. Contrary to my hypothesis, fragile papershell was more likely to occur in downstream areas but in reaches with thin riparian corridors, whereas Wabash pigtoe occurred in areas heavily influenced by agriculture or pasture and with narrow riparian corridors.

My models predicting bleufer, fragile papershell, and pimpleback presence suggested moderate support for my top ranked models; however, the explained deviance

Table 3.8 Matrix of *r*-values for Spearman's rank correlation coefficient related species densities with abiotic factors. Values of |*r*| ≥ 0.70 (indicated by asterisk) are considered multicollinear for landscape analyses. 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

values (pseudo R^2) indicated that the models explained very little variation in variables for bleufer, fragile papershell, and pimpleback presence (Table A 3.1). The weak patterns observed in the data did indicate that bleufer was most likely to occur in downstream reaches (drainage area: $\bar{x}$ = 2,360 km^2, SD= 1,765), and in channels of moderate sinuosity (WD: $\bar{x}$= 23.67, SD = 4.64). 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), whereas, pimpleback was most likely to occur in downstream reaches (drainage area: $\bar{x}$ = 2,298 km^2, SD= 1903) 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.

There was substantial support for one hypothesis predicting Wabash pigtoe presence (Table 3.9). The supported model (ΔAICc = 0, w_i = 0.94) indicated occupancy related to narrower riparian corridors ($\bar{x}$= 116 m) when compared to absent locations ($\bar{x}$= 138 m) and all available sites ($\bar{x}$= 127 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 similar influence (riparian corridor width $\bar{\theta}$= 3.89 and land use $\bar{\theta}$= 3.69) on mussels and Akaike weight suggested the top model had a 94% chance of being selected. The explained deviance indicated the model was adequate at predicting Wabash pigtoe presence (pseudo R^2= 36%).

Models predicting species densities

Results from the AICc model rankings indicated several habitat variables were influential to species densities. Drainage area, width-to-depth ratio, and shale lithology were selected most often to influence species densities, occurring in 83% (five of six) of the top ranked models. All species except Wabash pigtoe included drainage area as a top variable. Species densities were highest in the downstream reaches of the study area.

Table 3.9 AIC model hypotheses ranking for Wabash pigtoe presence. *K* is the number of estimable parameters, which includes the independent variables, a penalty term multiplier (2 by default) for increasing model complexity, AICc is AIC corrected for small sample size, Δ*i* = AICc differences, *wi* = Akaike weights, and Log-lik is the log likelihood, and pseudo R^2 indicates how well the model explains the response variable variation. Models are listed in descending order based on observed support (top ranked models Δ*i* ≤ 2, represented by an asterisk). A "+" indicates the covariates are additive in the model. Drain= drainage area, HEL= proportion of highly erodible land, Rip= riparian corridor width, Land= proportion of agriculture/pasture land, and Bank= bank erodibility.

Species	Description	*K*	AICc	Δ_i	w_i	Log-lik	R^2
Wabash pigtoe	Rip+Land*	4	32.31	0	0.94	-12.58	0.36
	Land	3	38.97	6.66	0.03	-17.21	0.30
	Drain+Rip	4	39.85	7.54	0.02	-16.35	0.27
	HEL+Land+Bank	5	43.76	11.45	0.01	-15.3	0.25

My models predicting bleufer and fragile papershell densities hypotheses showed only moderate support for the top ranked models. The pseudo R^2 values indicated that the models explained very little variation in bleufer and fragile papershell densities (Table A 3.2). My data indicated bleufer densities were highest downstream (5,860 km^2), in areas of wide riparian corridor (196 m) and where width-to-depth ratios were moderate (22-26; Fig. 3.5). Fragile papershell densities were highest downstream (5,813 km^2) and where width-to-depth ratios were moderate (22-24) and percent shale was relatively low (11%-45%; Fig. 3.6).

There was only substantial support for one hypothesis predicting density for both pimpleback and Wabash pigtoe (Table 3.10). Model ranking for pimpleback (ΔAICc = 0, w_i = 0.88) and Wabash pigtoe (ΔAICc = 0, w_i= 0.94) indicated there was substantial support for only one model. Pimpleback density was greatest in the downstream portion of the study area (drainage area= 5,813 km^2, Fig. 3.7). 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 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%; Fig. 3.8). 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 indicated model fit was very good (pseudo R^2= 65%).

Models predicting mussel-bed presence

Three of the four GLM models predicting mussel-bed presence were ranked high, however, the pseudo R^2 indicated that the models explained very little variation in mussel bed presence and were generally poor predictors of mussel-bed presence (Table A 3.3). My data 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).

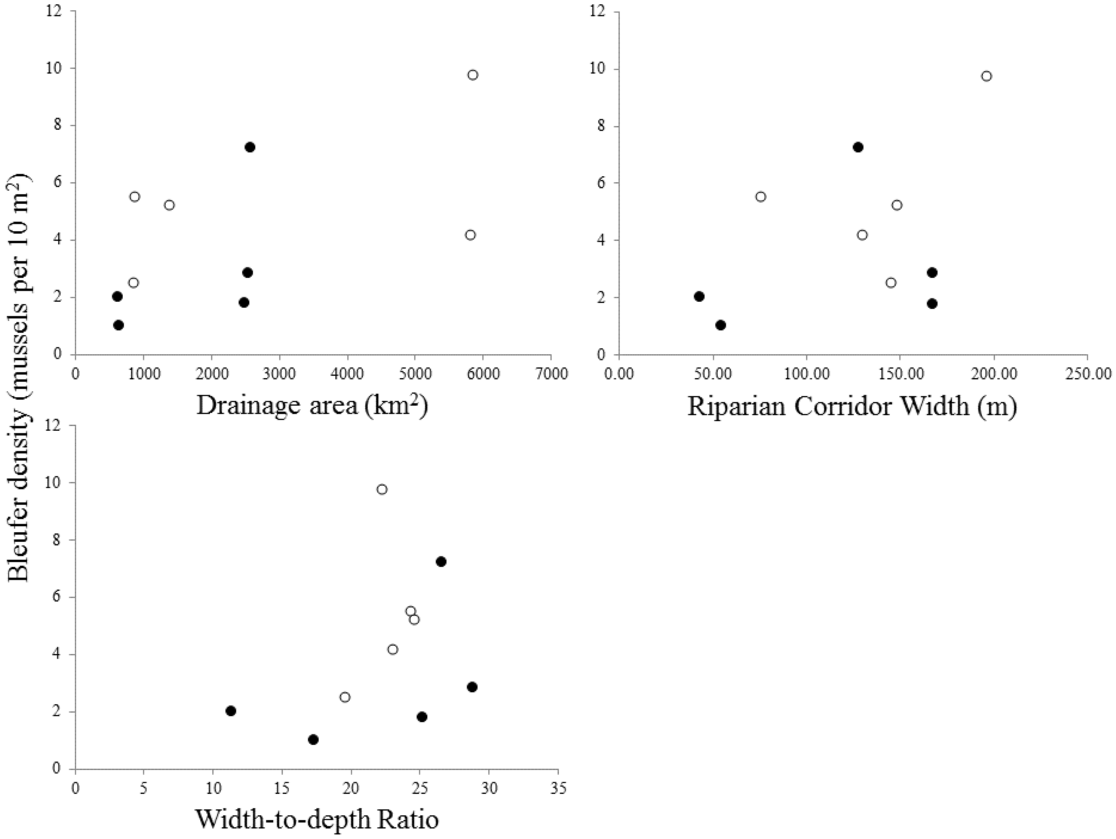

Figure 3.5 The relationship between bleufer density and drainage area, riparian corridor width, and width-to-depth ratio. Each point represents one sample location with black points associated with samples from the Clear Boggy River and white points with samples from the Muddy Boggy River.

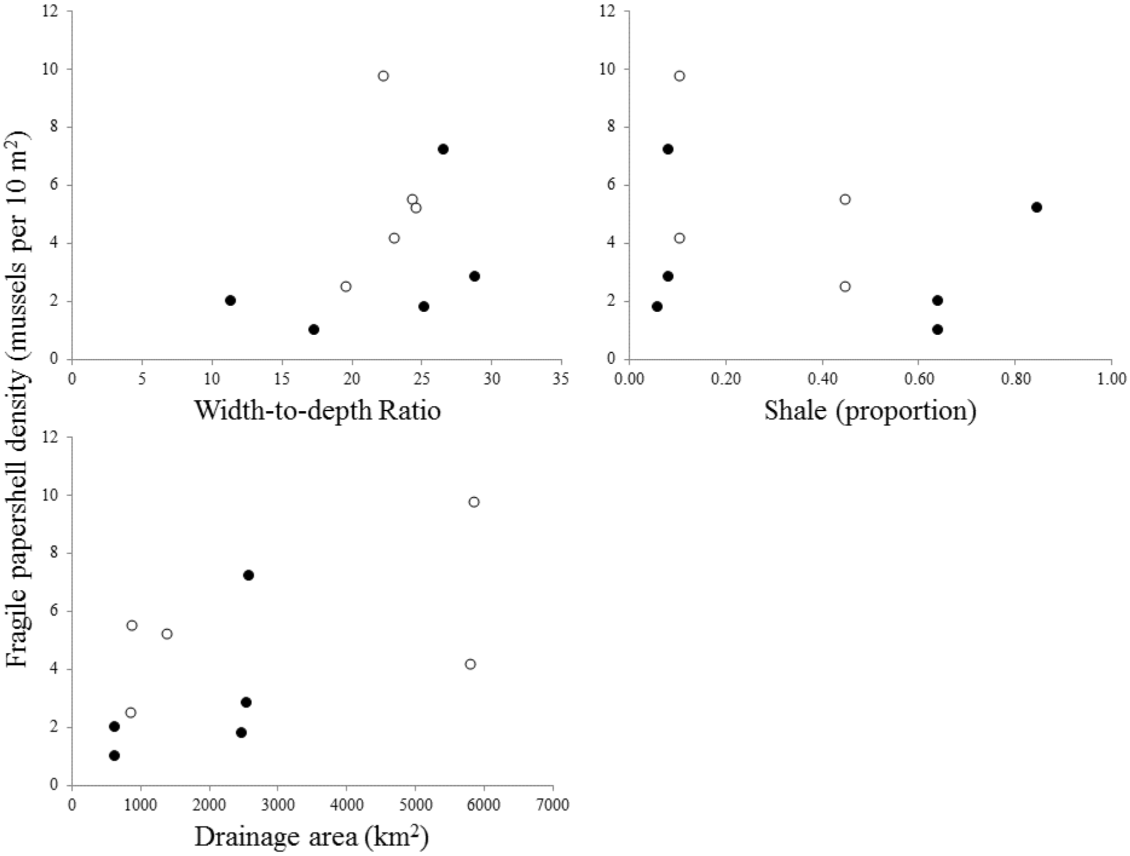

Figure 3.6 The relationship between fragile papershell density and width-to-depth ratio, proportion of shale lithology, and drainage area. Each point represents one sample location with black points associated with samples from the Clear Boggy River and white points with samples from the Muddy Boggy River.

Table 3.10 AIC model hypotheses ranking for pimpleback and Wabash pigtoe densities. *K* is the number of estimable parameters, which includes the independent variables, a penalty term multiplier (2 by default) for increasing model complexity, AICc is AIC corrected for small sample size, Δi = AICc differences, wi = Akaike weights, and Log-lik is the log likelihood, and pseudo R^2 indicates how well the model explains the response variable variation. Models are listed in descending order based on observed support (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, and Sub= substrate.

Species	Description	*K*	AICc	Δ_i	w_i	Log-lik	R^2
Pimpleback	Drain*	3	65.84	0	0.88	-27.92	0.39
	Geo+Forest	4	70.79	4.95	0.07	-27.39	0.30
	Drain+Geo	4	71.72	5.88	0.05	-27.86	0.28
	Drain+Forest+Sub	5	79.57	13.73	0	-27.28	0.25
Wabash pigtoe	Land*	3	77.14	0	0.94	-33.57	0.65
	WD+Rip	4	82.56	5.42	0.06	-33.28	0.36
	Forest+WD+Sub	5	92.51	15.37	0	-33.76	0.27

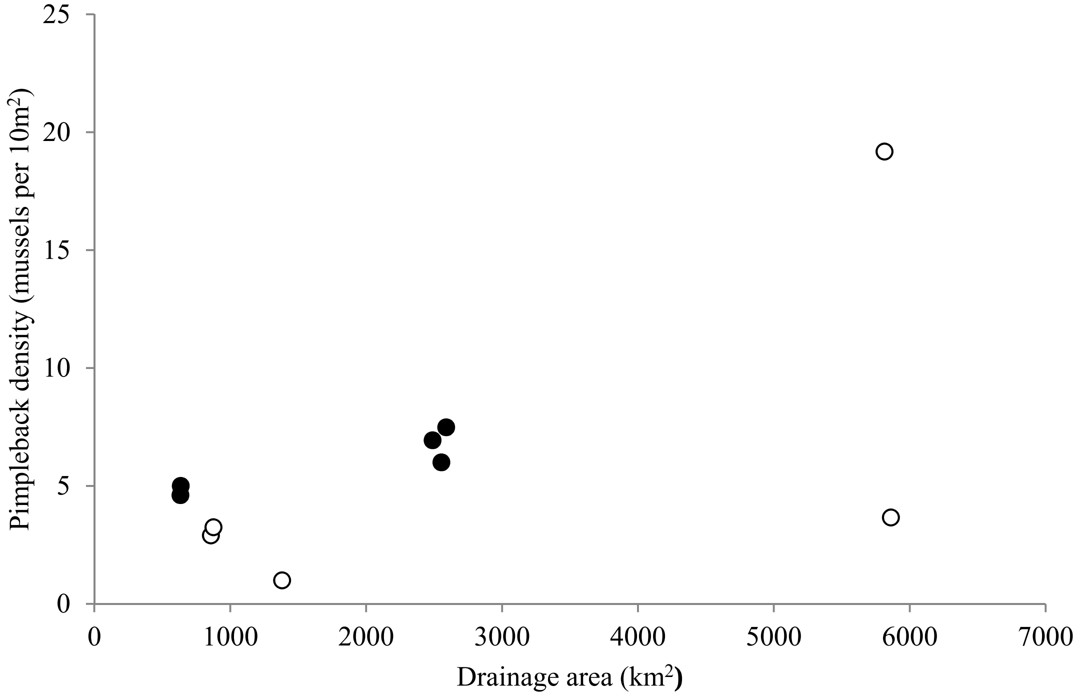

Figure 3.7 The relationship between pimpleback density and drainage area. Each point represents one sample location with black points associated with samples from the Clear Boggy River and white points with samples from the Muddy Boggy River.

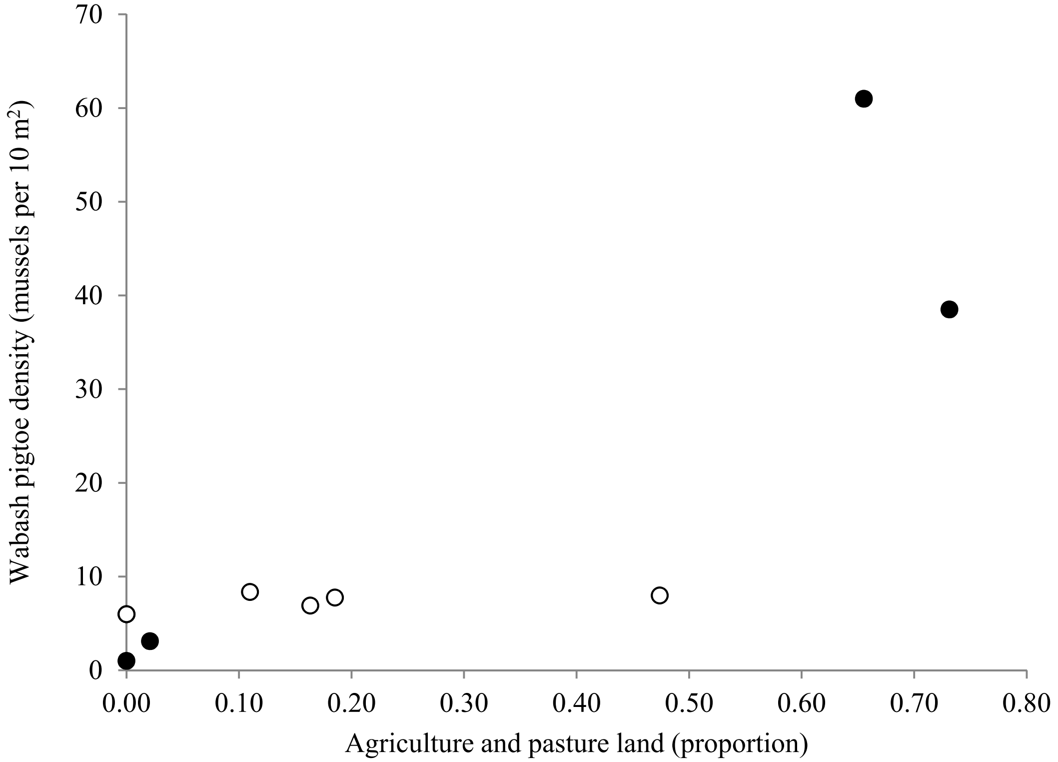

Figure 3.8 The relationship between Wabash pigtoe density and agriculture and pasture land. Each point represents one sample location with black points associated with samples from the Clear Boggy River and white points with samples from the Muddy Boggy River.

DISCUSSION

Some of my landscape models show how interactions between landscape and local habitat factors can influence persistence of freshwater mussels. I 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 excess fine sediment from entering the channel (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 increased 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). Wegner (1999) suggested riparian corridors of 30-100 m wide would adequately control sediment and provide optimal habitat and buffering capacity in most streams. Based on my findings, mussel introductions into rivers draining agriculture and pasture lands would be more successful when introduced into areas where riparian corridors are ≥ 100 m. Areas of wide riparian corridors were most conducive to higher mussel presences and densities.

The models I developed to predict mussel densities were often better fits to my data than those developed to predict mussel-bed and species presence (with the exception of Wabash pigtoe presence). One explanation for this may be how I defined a mussel bed. Mussels in my study rivers occurred in lower abundances 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. I considered a mussel bed an area with a mussel density of >5 per m^2 and covering 300 m^2 to be very large. Another confounding factor relates to the differences in stream characteristics between my study sites and the locations of most published studies. Supporting evidence for hypothesis development came primarily from clear stream systems in different geographic regions where factors driving distributions may differ (South Fork Eel River, CA, Howard and Cuffey 2003; River Basin, SE MI, McRae et al. 2004; southeastern, MI, Strayer 2006). This suggests more landscape studies would be beneficial because of the range of conditions these species' occupy. A third confounding factor may be the apparent ubiquitous use of upstream and downstream areas by some of the species studied (e.g., Wabash pigtoe, pimpleback). The species that showed the strongest relationships were those that demonstrated obvious longitudinal preferences (e.g., Wabash pigtoe). Not surprisingly, this was also true for my 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 my study (e,g,. shear stress, Daraio et al. 2010; bed stability, French and Ackerman 2014) or biotic factors (Schwalb et al. 2012) that were not accounted for in the models because fish were not sampled at all of the bed locations.

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) and has previously been found to influence freshwater mussel distributions (Strayer 2006, Atkinson et al. 2012). Stream size influences the longitudinal position of many mussel communities and there is a predictable shift in community composition as you move downstream from the headwaters (Atkinson et al. 2012). More often, mussels found in headwaters are smaller and short lived, whereas species downstream are larger and longer lived, likely because of the greater environmental variability exhibited in the headwaters (Atkinson et al. 2012, Haag 2012). My findings support this notion as I found bleufer, a long-lived and large mussel species, had greater densities downstream, whereas Wabash pigtoes, a smaller and shorter-lived species had greater densities upstream. Further, habitats exhibiting greater bed stability (i.e., downstream) 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 hydrologically stable allowing for mussel-bed establishment and persistence (Widdows et al. 2002) and preventing 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 my 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.

Side-scan sonar results were incorporated into my landscape models but data were not completely representative of the entire deep-water available habitat. The side-scan data were taken from the downstream portion of the Muddy Boggy River and do represent the deep-water habitat in the entire system. However, because most species occupied both rivers and models indicated preferences for downstream areas, the effect on model performance is likely negligible. The relative importance of more fine-scale habitat features would be more likely to be underrepresented because I did not include side-scan sonar data from the Clear Boggy River. Even so, some of the fine-scale data associated with deeper-water sites would still have been included because I still sampled the shallower waters within those sections. The most likely bias associated with how I included deep-water habitat would relate to the results reported on diversity where some species could be missed with or without the inclusion of side-scan sonar data. Comparing my data to historic data (Isely, 1925; Valentine and Stansbery, 1971; and Branson 1982) reported by Oklahoma Department of Wildlife Conservation (2005) on species presence in the Boggy Rivers, I sampled ~75% (14 of 19 species) of the mussels that were documented to occur in the rivers. However, it is unknown how much technique versus actual species loss over time may have influenced diversity.

Like others, I hypothesized fish-host presence to be an important factor influencing mussel distributions (Vaughn and Taylor 2000, Schwalb et al. 2012, Daniel and Brown 2013). I 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 (freshwater drum; Daniel and Brown 2013) making this biotic factor much more important than it might be for other species with multiple hosts (Daniel and Brown 2013, Cao et al. 2013, Stoeckl et al. 2015). Increases in the number of host fish would likely increase reproductive success and influence the distribution of species (Daniel and Brown 2013, Cao et al. 2013, Stoeckl et al. 2015). Glochidia remain attached to the gills or fins of their host fish 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). Additionally, fish-host presence is another reason species numbers are typically greater in the downstream portion of rivers. Fish abundances and species diversity were greater downstream which relates to an increased likelihood of mussel species numbers increasing in those same areas. My results, however, should be interpreted with caution because I sampled fish at eight sites so the scope of the analyses was limited. Future research would benefit from increasing the number of study sites to examine the influence of fish host on mussel presence.

Models for fragile papershell, pimpleback, and Wabash pigtoe were considered good predictors for species density (i.e., higher pseudo R^2 values). Fragile papershell and pimpleback both included drainage area in one or more of their tops models. This agrees with other studies that 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 the Clear Boggy. However, unlike pimpleback densities that were most influenced by drainage area, fragile papershells were also negatively related to shale lithology 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, higher amounts of shale lithology would increase pH acidity levels (Meybeck 1987) and that could be problematic for fragile papershells because their thin shells could be negatively affected (i.e., inhibit shell development or dissolve the calcium in the shell) (Watters 1994b). Fragile papershells typically occur in areas of moderate width-to-depth ratios (22 – 24; Combes and Edds 2005, Zigler et al. 2012). Moderate width-to-depth ratios typically relate to greater flow stability, thereby reducing the effects of shear stress (Rosgen 1994). The top-ranked model predicting Wabash pigtoe densities reinforced my hypothesis of a positive relationship between densities and modified lands. Wabash pigtoes are more tolerant of excess fine sediments (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).

My hypotheses predicting bleufer densities were inadequate suggesting more exploratory analyses may be beneficial. 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). Bleufer is commonly found in a variety of substrate types (Murray and Leonard 1962, Oesch 1984, Howells et al. 1996) suggesting substrate may be a poor predictor. I found drainage area was positively related to bleufer densities, confirming what others have reported (Miller and Payne 2001, Combes and Edds 2005). Additionally, width-to-depth ratios were included in my second top models. Drainage area and width-to-depth ratios likely relate to increased bleufer survival in reaches where hydrology is more stable allowing for reduced desiccation and displacement (Widdows et al. 2002, Strayer 2006, Atkinson et al. 2012). Models for bleufer may be improved by adding factors that are typically associated with drainage area such as hydrologic metrics and water temperature, which are likely important based on the size and longevity of bleufer (Widdows et al. 2002, Archambault et al. 2014, Daraio et al. 2014). The other variables (i.e., riparian corridor width, proportion of shale) I included in my *apriori* models were based on literature evaluating general mussel distributions (not specific specific) (Wenger 1999, Arbuckle and Downing 2002). This would indicate that including major factors that influence mussel populations is not well suited to identifying specific influences on individual species. Future exploratory studies on factors influencing bleufer densities, would increase our understanding of their distributions.

Increasing our knowledge about the factors influencing the distribution of freshwater mussels is important to developing effective conservation efforts. Propagation and reintroduction or introduction is a current focus of the conservation of mussels (Thomas et al. 2010, Carey et al. 2015). Unfortunately, only half of the current reintroductions or introductions of mussels 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 ineffective *a priori* evaluation of suitable habitat conditions at multiple spatial scales (Cope and Waller 1995, Peck et al. 2007). The results of my 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 that has a substantial amount of agriculture and pasture land, areas with wide riparian corridors (> 100 m) would be reasonable introduction locations. More importantly, selecting a more tolerant native species would be appropriate and my research suggests Wabash pigtoe to be a likely candidate.

This study provides insight into the factors that 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 et al. 2013, Davis et al. 2013) have found relationships between presence and channel slope or shear stress, particularly for the juvenile life stage (e.g., snuffbox *Epioblasma triquertra,* rainbow mussel *Villosa iris,* wavy-rayed lampmussel *Lampsilis fasciloa,* and eastern pondmussel *Ligumia nastua,* 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). 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 likely 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.

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Table A 3.1 AIC model hypotheses ranking for bleufer, fragile papershell, and pimpleback presence. *K* is the number of estimable parameters, which includes the independent variables, a penalty term multiplier (2 by default) for increasing model complexity, AICc is AIC corrected for small sample size, Δi = AICc differences, *wi* = Akaike weights, and Log-lik is the log likelihood, and pseudo R^2 indicates how well the model explains the response variable variation. Models are listed in descending order based on observed support (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	Description	*K*	AICc	Δ_i	w_i	Log-lik	R^2
Bleufer	Drain+WD*	4	31.44	0	0.7	-12.15	0.30
	Geo+Land+WD	5	34.7	3.26	0.14	-12.35	0.14
	Drain+HEL	4	35.27	3.83	0.1	-14.06	0.22
	HEL+Rip	4	36.5	5.07	0.06	-14.68	0.15
Fragile papershell	Drain+Rip*	4	34.65	0	0.78	-13.75	0.21
	Drain+WD+HEL	5	37.53	2.88	0.18	-13.76	0.08
	Drain+Sin+HEL	5	41.37	6.72	0.03	-15.69	0.13
	Rip+HEL+Bank	5	43.08	8.43	0.01	-14.96	0.19
Pimpleback	Drain*	3	34.89	0	0.45	-15.17	0.06
	Drain+HEL+Bank*	5	35.8	0.91	0.28	-12.9	0.20
	Geo+Forest*	4	36.08	1.19	0.25	-14.47	0.14
	Drain+Geo+WD	5	41.07	6.17	0.02	-13.95	0.11

Table A 3.2 AIC model hypotheses ranking for bleufer and fragile papershell densities. *K* is the number of estimable parameters, which includes the independent variables, a penalty term multiplier (2 by default) for increasing model complexity, AICc is AIC corrected for small sample size, Δi = AICc differences, *wi* = Akaike weights, and Log-lik is the log likelihood, and pseudo R^2 indicates how well the model explains the response variable variation. Models are listed in descending order based on observed support (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, Sin= sinuosity, and Sub= substrate.

Species	Description	*K*	AICc	Δ_i	w_i	Log-lik	R^2
Bleufer	Drain+WD*	4	66.49	0	0.36	-25.24	0.24
	Drain+Rip*	4	66.66	0.17	0.33	-25.33	0.21
	Geo+Sub*	4	66.81	0.33	0.31	-25.41	0.16
	Drain+Sin+Geo	5	75.62	9.13	0	-25.31	0.24
Fragile papershell	Geo+WD*	4	68.26	0	0.37	-26.13	0.26
	Drain+Geo*	4	68.41	0.15	0.35	-26.21	0.24
	Drain+WD*	4	68.89	0.63	0.27	-26.45	0.36
	Drain+WD+Geo	5	77.25	8.98	0.01	-26.12	0.26

Table A 3.3 AIC model hypotheses ranking for mussel-bed presence. *K* is the number of estimable parameters, which includes the independent variables, a penalty term multiplier (2 by default) for increasing model complexity, AICc is AIC corrected for small sample size, Δ*i* = AICc differences, *wi* = Akaike weights, and Log-lik is the log likelihood, and pseudo R^2 indicates how well the model explains the response variable variation. Models are listed in descending order based on observed support (top ranked models Δ*i* ≤ 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.

Description	K	AICc	Δ_i	w_i	Log-lik	R^2
Drain+Land*	4	62.61	0	0.32	-27.99	0.05
Drain+HEL+Land*	5	62.66	0.05	0.31	-26.79	0.10
Rip+Bank+HEL*	5	62.86	0.25	0.28	-25.6	0.12
Drain+Geo+Sin	5	65.23	2.62	0.09	-28.07	0.07

VITA

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