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Assessing Freshwater Mussels (Bivalvia: Unionidae) in South Dakota and Identifying Drivers of Assemblage Variation

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ASSESSING FRESHWATER MUSSELS (*BIVALVIA: UNIONIDAE*) IN SOUTH DAKOTA AND IDENTIFYING DRIVERS OF ASSEMBLAGE VARIATION

BY

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This thesis is approved as a creditable and independent investigation by a candidate of the Master of Science in Biological Sciences degree and is acceptable for meeting the thesis requirements of this degree. Acceptance of this thesis does not imply the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT

ASSESSING FRESHWATER MUSSELS (*BIVALVIA: UNIONIDAE*) IN SOUTH DAKOTA AND IDENTIFYING DRIVERS OF ASSEMBLAGE VARIATION

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Native freshwater mussels (Family: Unionidae) are among the most threatened groups of freshwater fauna on Earth. Approximately 35 species have gone extinct since the 1900s and 72% of remaining species are considered endangered, threatened, or species of special concern. Unionid research can begin by establishing species presence and distributions via surveys. Objectives for this study were to 1) implement the first comprehensive unionid survey for South Dakota to assess distribution, composition, and decline, 2) estimate assemblage density and determine local versus broad scale habitat drivers of assemblage variation, and 3) determine areas of unionid conservation priority in South Dakota. Mussels were qualitatively sampled in 2014 and 2015 from wadable and perennial streams at 202 randomly generated sites proportionately distributed throughout 14 major river basins in South Dakota. We found a total of 1152 individuals and 15 unique species with significant differences in richness and abundance between eastern and western halves of the state. Of the 202 survey sites, 91 showed evidence of unionids and 44 sites had live mussels. At sites where live mussels were encountered (n=44), quantitative adaptive cluster sampling was conducted during 2016 to estimate population densities and environmental drivers of assemblage variation. Average density was found to be 0.15 mussels m^{-2}. Non-metric multidimensional scaling was utilized to evaluate and estimate local, in-stream versus broad scale habitat drivers of assemblage variation of the 44 quantitatively sampled sites. Silt, fine gravel, sand, current velocity, and conductivity were significant in driving the assemblages. Fish hosts were found not to limit mussel distributions, instead, widespread land conversions to cultivated crop agriculture may be influencing assemblage distributions. Priority conservation areas were determined via a previously published ranking system. Conservation priority analysis of sites revealed conservation and management efforts would be most useful if focused in basins east of the Missouri River as the most abundant, rich, and diverse assemblages occur there. Most of the sites were found to overlap with Conservation Opportunity Areas defined by South Dakota Fish, Game & Parks. Collectively throughout the 2014-2016 surveys, we encountered 17 species, which was a 53% decline from the 36 species surveyed historically in South Dakota.

CHAPTER 1: GENERAL INTRODUCTION

Background

Freshwater ecosystems are delicate environments supporting approximately 10% of all known species despite occupying <1% of the Earth's surface (Dudgeon et al. 2006, Strayer and Dudgeon 2010). Approximately 20% of freshwater species are already extinct and the fragile nature of aquatic ecosystems is easily disrupted as exemplified in recent reports of freshwater biodiversity extinctions (Ricciardi and Rasmussen 1999, Bogan 2006, Strayer 2008, Haag and Williams 2014). Rapid growth of the human population has increased the number of activities surrounding freshwater streams and rivers in North America, proliferating the pressures put on freshwater ecosystems (Richter et al. 1997, Strayer and Dudgeon 2010). Anthropogenic influences aided the recent extinction of 123 freshwater species in North America, putting the extinction rate of freshwater faunas at 5 times that of terrestrial faunas (Ricciardi and Rasmussen 1999). Dudgeon et al. (2006) identified overexploitation, water pollution, flow modification, species invasions, and habitat degradation as the top 5 major threats to freshwater biodiversity. While overexploitation is typically pertinent to vertebrate species, the other 4 threats are common to all freshwater faunas (Dudgeon et al. 2006). Flow modification, habitat degradation, water pollution, impoundments, wide spread land use changes, and freshwater invasive species (e.g. *Dreissena polymorpha*) have spread via anthropogenic activities (Ricciardi and MacIsaac 2000, Allan 2004). Understanding how habitat alterations influence declines in aquatic biodiversity is important to the conservation of freshwater fauna globally.

North America has the most diverse unionid fauna on the planet, home to approximately 297 of the 820 species (1/3 of entire fauna) globally described (Lydeard et al. 2004, Strayer et al. 2004, Haag 2012). Native freshwater mussels (Family: Unionidae) top the list as one of the most imperiled freshwater faunal groups in North America. Freshwater mussels have seen recent species decline as 213 unionid species (71.7%) are considered endangered, threatened, or of special concern, and 35 species have become extinct since the 1900s (Williams et al. 1993, Ricciardi and Rasmussen 1999).

Ecosystem services provided by mussels include increased water clarity, sediment stability, biodeposition, nutrient cycling, nutrient contribution (empty shells), and food resources for small mammals, fish, and birds (Vaughn and Hakenkamp 2001, Gutiérrez et al. 2003, Zimmerman and de Szalay 2007, Vaughn et al. 2008). The ability to effectively provide these ecosystem services largely depends on assemblage biomass and environmental variables such as stream size, flow, surface geology, and substrate type (Vaughn 1997, Thorp and Covich 2010). Mussels can form dense assemblages of 100 m^{-2} (Thorp and Covich 2010) and ecosystem services are most beneficial when assemblages are at high densities, which allows more individuals to contribute services (Negus 1966, Vaughn et al. 2004). Unionids occur in a variety of habitats with permanent water, but primarily lotic systems. Within streams and rivers, mussels inhabit multiple habitat types including pools, runs, and riffles with a variety of substrates including mixed mud, sand, and gravel causing naturally patchy assemblage distributions (Thorp and Covich 2010).

Unique life history traits increase mussel vulnerability to imperilment. Due to a largely sedentary lifestyle, mussels require an obligate host for their glochidial larva, which facilitates dispersal, genetic diversity, and species vitality. The complex unionid lifecycle involves many crucial steps. Males release sperm into the water column, which is taken in through intake valves by nearby females. Fertilized eggs are brooded in the marsupium (gills) of the female until they reach a parasitic glochidial stage that requires a fish to serve as a dispersal agent. The glochidia must attach to the fins and/or gills of a particular species of fish in order to continue growing. If the glochidia do not attach to the right species of fish, its immune system will kill the young mussel. After the mussel infects the host, the glochidia encapsulate themselves into a phoretic state (only the small glochidia <100 µm obtain nutrients from the host) on the skin, gills, and/or fins of the host fish and the free-living larvae then drop off after a few weeks to a month. After release from the fish, juveniles settle to the bottom and root themselves into the benthic substrate to continue development to adults. Only if the glochidia land in a suitable habitat that allows immediate burrowing, will the lifecycle continue (Thorp and Covich 2010, Haag 2012). Different species of unionids require a particular to many species of fish in order for the glochidia to transform successfully. If the correct fish host species are not present, the mussels will not be able to reproduce.

Another biotic impact to mussels is the introduction of exotic species such as *Dreissena rostriformis bugensis* (quagga mussels) and *Dreissena polymorpha* (Zebra mussels) to North America. *D. polymorpha* introductions have resulted in devastating effects and are a cause of rapid extirpations of native unionids (Schloesser et al. 1996, Ricciardi et al. 1998). *D. polymorpha* reproduce and release millions of free-living veligers (juvenile zebra mussels) into the water column at the same time of year as unionids begin to extend their shells from the sediment to feed and reproduce. This timing of life histories allows the *D. polymorpha*, which actively search out hard substrate, to attach and successfully colonize on unionids. Upon the colonization of unionid shells, which can be a 4-6 cm layer over the entire shell, the *D. polymorpha* inhibit valve movement, cause deformities, and suffocate unionid siphons (Schloesser et al. 1996). This results in the reduction of food availability by means of direct interference of filtering as well as indirect interference since zebra mussels tend to reduce overall phytoplankton abundance in the water column (Schloesser et al. 1996).

Mussels are primarily filter feeders, meaning they obtain nutrients via siphoning water through intake valves (Thorp and Covich 2010). Unionids can filter a high volume of water that can exceed daily stream discharge, thus large assemblages can increase water clarity by reducing phytoplankton abundance and particulate organic matter in the water column (Haag 2012). Filtering out necessary food sources (phytoplankton, zooplankton, bacteria, fine organic detritus, and dissolved organic matter) can also become problematic for mussels as filter feeding may lead to the bioaccumulation of toxic contaminates in the water (Naimo 1995). Chemical toxins enter the water and are absorbed onto suspended particles which are filtered, leading to higher mortality rates (Naimo 1995). Toxic chemicals can be introduced to a stream or river system from a variety of ways, but widespread land use change may influence chemical input the most.

Land use change, river modification, and waste discharge from early European settlement produced massive sedimentation, pollution, and aquatic habitat degradation in North American riverine systems (Haag 2012). Land conversions for agronomic purposes are still increasing in a significant portion of the Western Corn Belt region at rates of 1.0-5.4% annually (Wright and Wimberly 2013). Included in the Western Corn Belt Region is South Dakota, where agriculture is prominent and nonpoint source run-off has impaired 60% of all assessed rivers and streams in the state (USEPA 2014). Richter et al. (1997) found that agricultural practices produce threats to aquatic ecosystems, which include nonpoint source pollution and habitat destruction. Nonpoint source pollution leads to sedimentation of the streambed, sediment loading, and nutrient loading. Sedimentation has been found to interfere with filter feeding activities, smothering of juveniles, and changes in substrate composition (Box and Mossa 1999, Haag 2012). Habitat destruction can occur from stream fragmentation, impoundments, channel alterations, introduced toxins, and exploitation, which have all been found to negatively impact mussel populations (Bogan 1993, Vaughn and Taylor 1999, Haag 2012).

Mussels are large organisms that can comprise 25% - 90% of total benthic biomass, sedentary, and long-lived (some species living over 100 years) which makes them easy targets for exploitation (Haag 2012). By the early 1850s, early European settlers began to commercially harvest freshwater mussels as an important economic source. Mussels were harvested for pearls starting in the late 1800s, but this practice subsided in the early 1900s due to rapid mussel depletion (Haag 2012). After the pearl rush, piles of discarded shells were found useful in making buttons. With the discarded shells and through additional mussel harvests, the American shell button industry began in the late 1800s. By 1912, 196 factories in 20 states were involved in the valued button manufacturing industry (Haag 2012). Harvest peaked in the United States at more than 50,000 tons in 1912 and averaged 20,000 tons per year from 1895-1950, resulting in mortality of at least 11 billion mussels (Haag 2012). The invention of the plastic button and depleted mussel stocks led to significant reductions in harvest by the 1950s (Haag 2012). The compounding effects of over-harvesting seen throughout recent human history have highly depleted abundant mussel populations and the impacts are still seen today (Bogan 1993, Williams et al. 1993, Strayer et al. 2004, Thorp et al. 2009, Haag 2012).

Unique biology and life history characteristics make unionids sensitive to multiple environmental factors and knowing the status of mussel assemblages can serve as a key indicator of potentially degraded stream environments. Understanding the locality and array of native mussel species in an area of interest can provide assemblage and habitat information used to help protect and conserve remaining populations.

Estimating mussel status in streams and rivers is required to detect assemblage and species changes and potential declines (Strayer et al. 2004). Qualitative and quantitative surveys are commonly used to evaluate mussel assemblages, evaluate presence or absence of species, assess assemblage density and variation, and determine preferential habitat. Recent mussel declines can be detected by comparing past surveys in any given spatial area to recent surveys conducted throughout the same areas.

South Dakota has had no statewide comprehensive unionid survey; only localized and limited surveys have found evidence of 36 species east of the Missouri River, including 3 federally endangered species: *Lampsilis higginsii* (Higgins Eye), *Leptodea leptodon* (Scaleshell), and *Quadrula fragosa* (Winged Mapleleaf) (Coker and Southall 1915, Over 1942, Perkins 1975, Hoke 1983, Perkins 1985, Perkins et al. 1995, Skadsen 1998, Perkins and Backlund 2000, Skadsen and Perkins 2000, Hoke 2003, Perkins and Backlund 2003, Perkins and Backlund 2004, Wall and Thomson 2004, Ecological Specialists 2005, Shearer et al. 2005).

Thesis objectives

The purpose of this study was to I) document the current distribution, species composition, and abundance of native freshwater mussels, and to assess unionid decline relative to historical surveys in South Dakota (*Chapter 2*), II) estimate assemblage density in streams with mussel assemblages and identify critical local and broad scale habitat drivers that explain much of the variation in among local and regional assemblage structure (*Chapter 3*), and (III) determine areas of unionid conservation priority across the state (*Chapter 4*).

Expected results will build an information base necessary to sustain mussels in South Dakota for future generations by taking inventory of these natural resources. Documenting the mussel resources in the state's rivers and streams will provide knowledge of the localities and status of unionid assemblages for conservation and protection efforts. In addition, data obtained from this project will provide possible recommendations for a long-term monitoring plan and information that can be used to develop educational materials for natural resource agencies.

CHAPTER 2: DISTRIBUTION, COMPOSITION, AND DECLINE OF UNIONID MUSSELS IN SOUTH DAKOTA, USA

ABSTRACT

North America is home to the world's most diverse native freshwater mussel fauna (Family: Unionidae) but approximately 72% of species are thought to be extinct or imperiled. Biological mussel surveys provide baseline information critical to future biodiversity conservation, yet a comprehensive survey has not been completed in the state of South Dakota. The purpose of this research was to survey the current distribution, composition, and potential decline of unionids within South Dakota. Statewide, we found evidence of 1152 individuals and 15 unique species from 202 stratified, random sites within 14 major river basins. Evidence of mussels was encountered at 91 (45%) of our sites and *Pyganodon grandis* (Giant Floater) was the most frequently encountered species. In eastern South Dakota, we encountered 1009 individual accounts that comprised 15 species, which was significantly different from the 143 individual accounts and 5 species found throughout the western half of the state. To examine potential statewide decline, we reviewed historic surveys (1915-2005) that encompassed localized areas throughout eastern South Dakota. We resurveyed 7 accessible sites and calculated average decline in richness of 1 species per 10 years. At a basin-wide scale, we compared our data with historical surveys and observed over 50% fewer species. Reasons for decline may be attributed to widespread land conversion, hydrological changes, invasive species, and habitat destruction. Overall, mussel declines in South Dakota appear similar to those described from other states in the United States.

INTRODUCTION

Declines in freshwater biodiversity have been documented to occur at rates faster than those observed from terrestrial ecosystems mainly due to anthropogenic impacts, which can reduce suitable habitat (Downing et al. 2010). One of the most threatened faunas worldwide is native freshwater mussels (Family: Unionidae) with an estimated global extinction rate of 1.2% per decade, substantially higher than that of all other faunal groups (Ricciardi and Rasmussen 1999). North America has the most diverse unionid fauna globally with approximately 300 species described, yet 35 of those species (16%) have gone extinct since the 1900s and 213 species (72%) are considered endangered, threatened, or of special concern (Williams et al. 1993, Ricciardi and Rasmussen 1999). Causes of mussel decline are complex and multifaceted, yet Downing et al. (2010) described water quality degradation, habitat destruction, and hydrological changes as the 3 most frequently occurring factors that influence mussel declines. A comprehensive unionid survey is needed in South Dakota as threats to mussels are becoming prevalent and widespread. Habitat destruction is occurring as grasslands are converted to cultivated agriculture (Johnston 2014) resulting in degradation of streams and rivers, and invasive *Dreissena polymorpha* (zebra mussels) are encroaching into the state.

Mussel decline is often detected via surveys as researchers assess species richness and abundance throughout a drainage basin or region. Mussel surveys have been implemented in all midwestern states (Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, and Ohio) and decline has been observed in each (Badra and Goforth 2003, DeLorme 2011, Fisher 2006, Grabarkiewicz and Gottgens 2011, Hoke 2011, MNDNR 2004, Obermeyer et al. 2006, Poole and Downing 2004, Roberts et al. 2008, Stodola et al. 2014), yet no comprehensive survey has been completed for South Dakota. Fifteen small-scale surveys have been implemented throughout the eastern portion of the state, but the majority of these surveys were completed between 1975 to 2005. Only 2 surveys were completed before 1975, which were poorly executed compared to the caliber of the other 12.

Our hypothesis was that native mussel species richness has declined throughout the state relative to the historic surveys. We initiated the first comprehensive, statewide unionid survey of South Dakota with the objectives of documenting presence/absence of species, describing assemblage structure (species richness and abundance), and detecting changes in assemblage structure relative to historic survey data.

METHODS

Study Area

South Dakota is roughly bisected by the Missouri River and 14 major river basins occur within the state boundaries (Figure 1). Formidable environmental differences exist between the eastern and western halves. Strong east-west precipitation and north-south temperature gradients produce distinct regional climates across South Dakota (Johnson 2005). River basins east of the Missouri River are physically different from those west of the river primarily due to the Wisconsin glaciation (Gewertz and Errington 2015). Basins in the eastern half have been glaciated and are characterized by a continental climate, mid to tall-grass prairie, and land cover that is currently dominated by cultivated agriculture (Auch 2014). Western basins have not been influenced by glaciation and are characterized by a semiarid climate, rolling plains with occasional buttes and badlands, and land is currently used mainly for livestock production (Sayer 2014). Streams and rivers in western South Dakota are prone to intermittency and flash flooding which is quite different than the more hydrologically stable streams and rivers in basins east of the Missouri River.

Field Surveys

A statewide freshwater mussel survey was executed during the summers of 2014 and 2015. Sampling sites (n=202) were randomly and proportionately generated based upon watershed land area using ArcGIS (10.1/2012, ESRI, California) to ensure no sampling bias toward a particular basin. Stream sampling sites were restricted to wadable, perennial mainstem and tributary sites throughout 6 river basins east of the Missouri River with 102 sites and 8 basins encompassing 100 sites west of the Missouri River. Sites where landowner permission could not be obtained or where there was a lack of flowing water were replaced with another random site within the same river basin. Seven sites were selected to resurvey from 6 different historical surveys (1975-2004), based upon landowner permissions and accessibility, thus not considered random.

Sites east of the Missouri River were surveyed from 4 June to 14 August 2014, while those west of the Missouri River were surveyed from 27 May to 27 July 2015.

Timed, qualitative searches were employed to survey mussel occurrence and species composition following the wadable rivers protocol of DeLorme (2011). Each site (n=202) was visited and searched for 2 person-hours starting from the nearest access point and moving in an upstream direction. All living mussels, empty shells, and shell fragments detected by visual and tactile means were collected for identification. All live mussels encountered were measured for length, width, depth, and photographed for documentation. Mussels not kept as vouchers for the South Dakota Aquatic Invertebrate Collection located at South Dakota State University, Brookings, SD, were returned to the stream. Those specimens difficult to identify in the field were returned to the laboratory for further identification.

Historical Surveys

For this study, we defined historical records as those collected on or before 2005, since 2005 was the last year a survey was completed in South Dakota. To detect mussel decline, we compared our survey results against all historical surveys (1915-2005) using 2 different approaches. We resurveyed 7 sites from historical surveys to directly evaluate change in species composition (Figure 1). Resurveyed sites were located east of the Missouri River since no formal observations had been documented from western basins. Decline was calculated using an average species richness change per year (ΔR_{yr}) since each historic survey was taken in a different year. This method was deemed to be the best estimate of change to encompass all revisit sites over time in order to make fair comparisons. The richness decline per year of resurveyed sites was calculated using:

$$\Delta R_{yr} = \frac{(Current\ species\ richness - Historic\ species\ richness)}{(2014 - Historic\ survey\ year)}$$

where '2014' was used since all revisit sites occurred east of the Missouri River, thus were surveyed during our first field season and 'historical survey year' was the year of the historic survey of interest.

We also compared assemblage changes at a basin-wide scale. Eleven historical surveys (1975-2005) (Perkins 1975, Perkins 1985, Skadsen 1998, Perkins et al. 1995, Perkins and Backlund 2000, Skadsen and Perkins 2000, Hoke 2003, Perkins and Backlund 2003, Wall and Thomson 2004, Ecological Specialists 2005, Shearer et al. 2005) had specific site locations and specimen counts for each site, which were compiled to obtain total species richness and abundance for each basin. Richness and abundance data for both historical and current surveys were compared using a paired t-test in Statistix (10.0/2013. Analytical Software, Tallahassee, FL).

For both the field and historic surveys, species classification was determined against the Integrated Taxonomic Information System, an online classification database (ITIS 2015). Mussels listed as "unknown" were either too young to identify, severely weathered, or fragmented shells. In an effort to standardize results for historic and current findings, empty valves that were counted as halves in the field or historical literature were combined to produce a composite number. For example if we found 3 valves of a species, those valves were recorded as 1.5 individuals. Species richness was determined as the sum of all species represented by empty shells and live specimens for the area of interest. Evidence at a site was determined by presence of shell fragments, valves, and/or live mussels. Abundance was determined as the sum of all empty shells and live specimens for the given area of interest. Each species encountered was assigned as a habitat and host fish generalist or specialist based upon Haag (2012).

RESULTS

Field Surveys

Our investigation indicated the occurrence of mussels in all 14 major river basins. Evidence of mussels occurred at 91 (45%) sites and live mussels occurred at 44 (22%) of the survey sites. A total of 15 species (Appendix I) were encountered from our survey, 11 represented by live specimens (Table 1). A total of 1151.5 live and empty shells were found throughout our survey, 606 of which were live specimens (Table 1). We found evidence of all 15 species in basins east of the Missouri River and 5 species in basins west of the Missouri River (Appendix I). Ten (67%) species encountered were considered fish host specialists, meaning the glochidia can only transform on a small subset of fish species (Haag 2012). Overall, mean species richness per basin was 4 with the highest richness in the James River basin (10 species) and the lowest richness in the Moreau, White, and Niobrara River basins (1 species each). In basins east of the Missouri River, we found evidence of a total of 1009 (562 live) specimens with a mean of 169.3 specimens collected per basin. We found 142.5 (41 live) specimens with a mean of 17.8 specimens per basin west of the Missouri River.

Mean abundance per basin was 82 specimens among all 14 river basins. The highest abundance of 442 specimens or 38% of all specimens encountered was found in the James River basin and the lowest abundance of one specimen (<1 % of total encountered) from the Niobrara River basin. The most abundant species encountered was *Pyganodon grandis* (Giant Floater), which represented 63% of all mussels found. Remaining species each represented no more than 10% of total abundance (Table 1). Local assemblages were typically dominated by 2 fish host and habitat generalist species (Haag 2012), *P. grandis* and *Lasmigona complanata* (White Heelsplitter), which comprised 73% of the total abundance for all basins. Fish host generalists are species of mussels that have glochidia that can transform on virtually all fish species and habitat generalists are those mussel species which can survive in impounded waters (Haag 2012).

Elliptio dilatata (Spike) was observed from the Bios de Sioux River in the Red River basin, representing a new state record. This was a resurvey site which was extensively sampled by Perkins et al. (1995) who found evidence of 5 species. We found 3 additional species (*E. dilatata, Amblema plicata* (Threeridge), and *Quadrula quadrula* (Mapleleaf)) at this site, all of which were represented by live specimens. Perkins et al. (1995) did find 1 species we did not encounter at this site, *Potamilus ohiensis* (Pink Papershell). A single valve of *Venustaconcha ellipsiformis* (Ellipse) was found in Split Rock Creek in the Big Sioux River basin near Brandon, South Dakota, which is also a new record for South Dakota.

Mussel decline

Statewide, a combined total of 36 species were identified from all historic surveys (1915-2005) including 3 federally endangered species: *Lampsilis higginsii* (Higgins Eye), *Leptodea leptodon* (Scaleshell), and *Quadrula fragosa* (Winged Mapleleaf) (Coker and Southall 1915, Over 1942, Perkins 1975, Hoke 1983, Perkins 1985, Perkins et al. 1995, Skadsen 1998, Perkins and Backlund 2000, Skadsen and Perkins 2000, Hoke 2003, Perkins and Backlund 2003, Perkins and Backlund 2004, Wall and Thomson 2004, Ecological Specialists 2005, Shearer et al. 2005). We encountered evidence of 15 species, a potential 58% decline in species richness since 1915. Historically, 7 species were found to comprise 73% of the total abundance among all mussel species: *Q. quadrula* (16%), *P. grandis* (15%), *Leptodea fragilis* (Fragile Papershell) (13%), *A. plicata* (11%), *Lampsilis siliquoidea* (Fatmucket) (11%), *L. complanata* (4%), and *P. ohiensis* (3%). We encountered 15 total species and only 2 species comprised 73% of total abundance among all species: *P. grandis* (63%) and *L. complanata* (10%).

Of the 7 resurveyed sites, 5 showed evidence of richness decline, 1 site increased in richness, and 1 site showed no change (Table 2) from historical richness. The Whetstone River site had the largest decrease with 4 fewer species than previously found by Perkins et al. (1995) (Table 2). Based on these 7 sites, there was an average decline in species richness of 1 species per 10 years. The most frequently encountered and abundant species historically and currently from the 7 resurveyed sites was *P. grandis*. The second most abundant species was previously *L. siliquoidea* but is now *L. complanata*.

Of the 11 historical surveys for basin-wide comparisons, 243 sites were identified throughout 6 basins (Big Sioux, James, Minnesota, Missouri, Red, and Vermillion) and our survey included 71 sites in the same basins (Table 3). Combined, the historical surveys (1915-2005) included 36 species, but only 30 species were encountered from these particular surveys (1975-2005) for comparison. We encountered 15 species, indicating a potential 50% decline in species richness for the comparison sites. Richness and abundance were found to be significantly different between historic and current records ($t = -2.24$, $p = 0.05$) and ($t = -2.63$, $p = 0.03$), respectively.

DISCUSSION

It is clear through the limited historic surveys that native mussels occurred throughout South Dakota, especially in the eastern half, yet no comprehensive statewide survey had been completed until now. After concluding the first inclusive statewide survey for South Dakota, which also included resurveyed historical sites and basin-wide historical comparisons, it appears mussel species richness and assemblage structure have changed and declined over the past 100 years from the first localized survey by Coker and Southall (1915). Species richness has decreased by 58% statewide and assemblage composition has shifted to be dominated by 2 fish host and habitat generalist species. The stark decline in species richness may suggest that habitat conditions in South Dakotan streams and rivers are degrading, possibly due to a variety of factors such as land-use changes, impoundments, habitat destruction, and host fish availability.

Unionid surveys have been completed in midwestern states (Iowa, Indiana, Illinois, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, and Ohio), most of which are included in the Western Corn Belt region of the United States. All have observed declines in species richness (Badra and Goforth 2003, MNDNR 2004, Poole and Downing 2004, Delorme 2011, Fisher 2006, Obermeyer et al. 2006, Roberts et al. 2008, Grabarkiewicz 2011, Hoke 2011, Stodola 2011). Highest declines in species richness were detected in watersheds that had experienced widespread land conversion to agricultural practices and suggested that species decline was strongly associated with increased levels of agricultural land use (Poole and Downing 2004, DeLorme 2011). Agricultural land use has been documented to be a common cause of habitat degradation as such land use practices cause increased nutrient and sediment loads into freshwater systems (Box and Mossa 1999, Saunders et al. 2002, Burdon et al. 2013, Lummer et al. 2016).

Included in the Western Corn Belt region, the state of South Dakota has witnessed recent and widespread land-use conversion from grassland to row crop agriculture (Johnston 2013, Wright and Wimberly 2013). Conversion from grassland to cultivated corn and soy crops is occurring throughout parts of the Western Corn Belt at rates of 1.0-5.4% annually, which is comparable to deforestation rates in Brazil, Malaysia, and Indonesia (Wright and Wimberly 2013). Increased land conversion to agricultural practices have been linked to declines in water quality, degraded habitat, sediment alterations, and changes in water hydrology all of which have been identified as causes of unionid impairment (Allan 2004, Downing et al. 2010, Lummer et al. 2016).

Freshwater mussel declines have been ascribed to a variety of anthropogenic stressors throughout history. Despite more than 5000 years of non-commercial human harvest, mussel diversity was primarily undiminished into the early 1900s, Commercial harvest then became prevalent (Haag 2012). It wasn't until around 1924, prior to widespread agriculture, that anthropogenic actions began to transform mussel habitat as dam installation greatly increased throughout North American rivers and began to decrease suitable habitat for remaining populations. (Haag 2012).

South Dakota impoundments are present in waterways across the state. Four mainstem dams exist along the Missouri River and thousands of small impoundments on tributaries flowing through private land no doubt influence mussel habitat and host fish distribution (Johnson et. al 1997). Even dams as low as 1 meter in height have been found to inhibit the distribution of mussels as they can create unnatural sedimentation and flow regimes as well as cause barriers to fish host locality and movement, thus inhibiting the ability for successful mussel recruitment (Watters 2000, Haag 2012).

The establishment of non-native freshwater species is recognized as one of the most serious threats to native species (Saunders et. al 2002). This can be especially true in the case of native fish species as they are commonly replaced by non-native fish (Moyle 1986, Saunders et al. 2002). Twenty-two nonindigenous fish species reside in South Dakota, which compete for limited habitat and resources with native host fish (Saunders et al. 2002, Hoagstrom et al. 2007). Loss of native fish hosts or even declines in their abundance could negatively impact mussel recruitment success. Ten mussel species we encountered were considered fish host specialists (Table 1), meaning they can only metamorphose on a small and particular subset of fish species (Haag 2012). This would suggest that many of the critical host fish are present; at least for those unionid species which still occur within the state. Additional data is needed to document any changes in fish host abundance.

Dreissena polymorpha (zebra mussel), an invasive mussel species, has recently been documented from the Missouri River in southeastern South Dakota. *D. polymorpha* individuals have high fecundity 10^4 - 10^6 eggs yr^{-1} (Walz 1978) and rapid dispersal rates, which allow them to outcompete native unionids. *D. polymorpha* have free swimming larvae and attach to almost any hard surface including unionids, up to 200 per individual, causing the unionid to suffocate and die of starvation (Haag 2012). As of now, *D. polymorpha* have not been found upstream of Gavins Point dam in Yankton, South Dakota, but if this species encroaches beyond this dam into the state's rivers and tributaries, native unionids will most likely be negatively impacted.

Our effort-based searches provided a representative means to evaluate species occurrence within major river basins using a probability-based design. There is always the possibility that some species were not encountered in our survey. Similarly, *V. ellipsiformis* and *E. dilatata* may have been extant in the state historically, but were not encountered during historic surveys. Additional research is needed to identify critical habitat needs of remaining mussel species and their fish hosts in prairie streams. Critical information is still needed to facilitate conservation efforts for optimal habitat with regards to the strategies of both mussel and fish hosts, which persist under hydrologically variable stream conditions. Our research completed the first comprehensive unionid survey in South Dakota and suggests that the statewide unionid structure is changing quickly, thus adequate conservation strategies are needed for the future survival of this group.

Table 1. List of all unionid mussels including live and empty shells collected from the 2014-2015 survey of South Dakota perennial, wadable streams and rivers. Species marked with a '*G*' are generalist species for host fish, and species marked with an '*S*' are specialists (Haag 2012). Location represents where the species was found, 'E' is east of the Missouri River and 'W' is west of the Missouri River.

		Basin(s) present															
Species	Location	Bad	Belle Fourche	Big Sioux	Cheyenne	Grand	James	Little Missouri	Minnesota	Missouri	Niobrara	Red	Vermillion	White	Number live	Total abundance	Relative abundance
Amblema plicata[G]	E			X									X	X	6	8.5	0.7375
Lasmigona complanata[G]	E,W		X	X		X	X		X	X			X	X	54	119	10.325
Pyganodon grandis[G]	E,W	X	X	X	X	X	X	X	X	X	X	X	X	X	328	725.5	62.95
Strophitus undulatus[G]	E								X						1	1	0.0868
Utterbackia imbecillis[G]	E,W	X		X			X			X			X	X	50	61	5.2928
Elliptio dilatata[S]	E												X		2	4	0.3471
Leptodea fragilis[S]	E			X										X	0	2	0.1735
Ligumia recta[S]	E						X								0	1.5	0.1301
Lampsilis siliquoidea[S]	E,W			X			X	X	X				X	X	20	56	4.859
Obliquaria reflexa[S]	E						X								0	1	0.0868
Potamilus alatus[S]	E,W				X		X			X			X	X	33	49	4.2516
Pleurobema sintoxia[S]	E								X					X	94	103.5	8.9804
Quadrula quadrula[S]	E						X			X			X		13	15	1.3015
Truncilla truncata[S]	E						X								1	1	0.0868
Venustaconcha ellipsiformis[S]	E			X											0	0.5	0.0434
Unknown	E									X			X		4	4	0.347
TOTAL															606	1152.5	100.0

Table 2. Species richness and total abundance of 7 sites resurveyed from historical literature to evaluate mussel assemblage changes overtime in eastern South Dakota.

Water body	Basin	Richness		Total abundance		Historic survey source
		Historic	Current	Historic	Current	
Vermillion River	Vermillion	6	5	52	10	Perkins (1975)
Big Sioux River	Big Sioux	1	0	1	0	Skadsen & Perkins (1995)
Bios de Sioux River	Red	5	7	85	22.5	Perkins et al. (1995)
Foster Creek	James	4	1	93	4	Wall & Thomson (2004)
Hidewood Creek	Big Sioux	3	3	8	2	Skadsen (1998)
Redstone Creek	James	3	1	67.5	7	Wall & Thomson (2004)
Whetstone River	Minnesota	8	4	42	45.5	Perkins et al. (1995)

Table 3. Comparison of historical mussel surveys (n = 11) to those observed from the current study by major river basin in eastern South Dakota. Based on these 6 basins, there was a 50% decline in species richness.

Basin		Number of sites	Richness	Abundance
Big Sioux	Historic	77	27	3128.5
	Current	20	7	119.5
James	Historic	57	23	7205
	Current	39	10	546.5
Minnesota	Historic	20	12	1622
	Current	6	8	32.5
Missouri	Historic	75	17	2121.5
	Current	26	5	206
Red	Historic	2	5	101.5
	Current	2	8	15
Vermillion	Historic	12	14	801
	Current	9	8	109.5

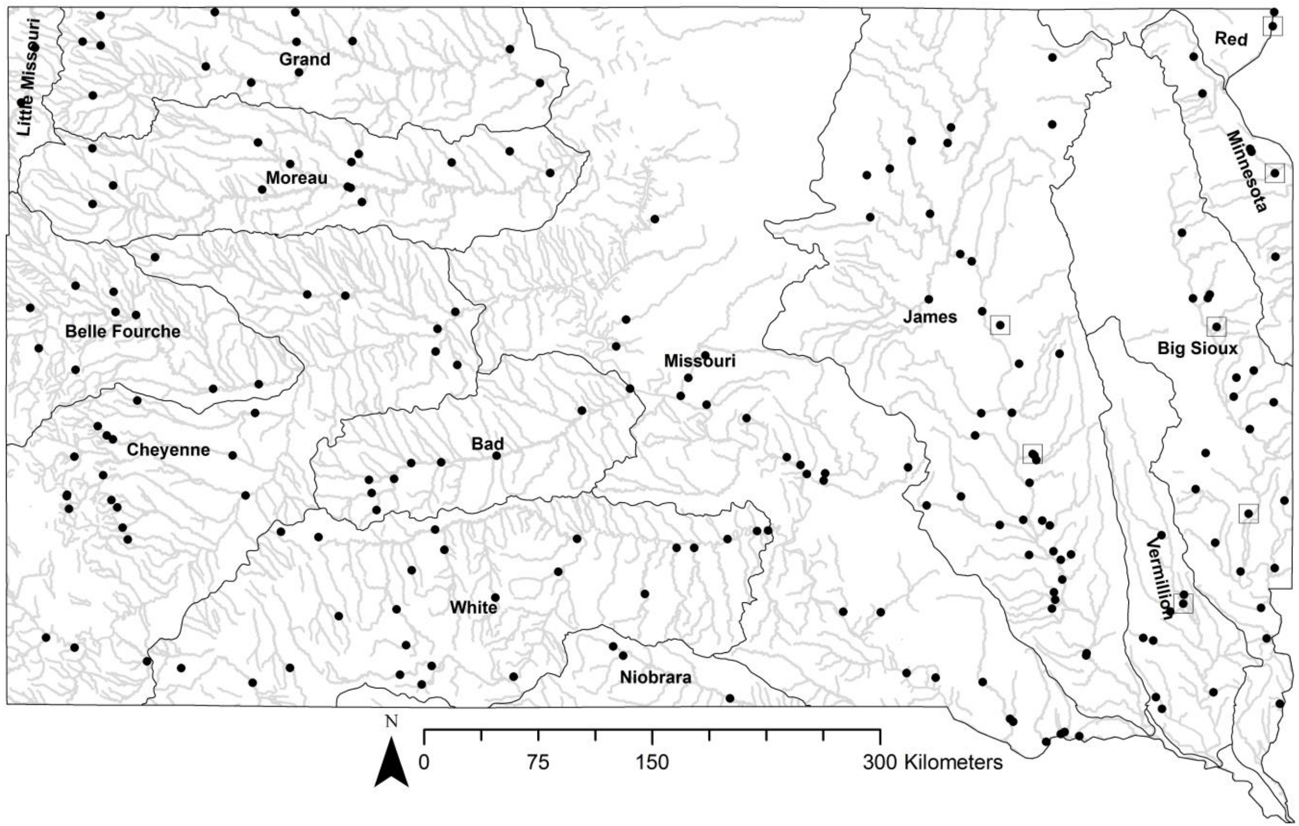


Figure 1. Map depicting mussel survey site locations in 14 labeled major river basins of South Dakota. Each survey site is represented by a dot and those with boxes surrounding the dot represent the historic resurvey sites (n=7) shown in Table 2.

CHAPTER 3. POPULATION DENSITY AND DRIVERS OF ASSEMBLAGE VARIATION OF UNIONIDS IN SOUTH DAKOTA

ABSTRACT

Habitat variables play influential roles in freshwater mussel (Family: Unionidae) distribution and abundance. With recent mollusk extinctions estimated to be higher than that of all other taxa combined and over half of those extinctions occurring in the United States, understanding assemblage density and habitat requirements are essential to mollusk conservation and management efforts. Our research identified 44 sites in South Dakota with the objectives to estimate assemblage density and evaluate the strength of local versus broad scale habitat drivers explaining assemblage variation in distribution and abundance. Mussel assemblage density and habitat variables at each site were quantified using adaptive cluster sampling. Mussel density averaged 0.15 mussels m^{-2} and ranged from 0 to 56 animals m^{-2} with a range of 0 to 5 species quadrat $^{-1}$. We utilized nonmetric multidimensional scaling to explore the relationship between local and broad scale habitat variables with mussel assemblage composition. Substrate (silt, fine gravel, and sand), current velocity, and conductivity were found to be the top 3 local habitat drivers of assemblage variation. Fish host distributions were not found to limit mussel distributions, but instead, increased levels of land conversion resulting in habitat alteration may play a role in assemblage composition and distribution throughout streams and rivers in South Dakota.

INTRODUCTION

Humans rely heavily on freshwater systems which has already led to intense flow modification, pollution, water removal, commercial exploitation, and widespread habitat degradation (Williams et al. 1993, Dudgeon et al. 2006, Burlakova et al. 2011). Such anthropogenic pressures on freshwater systems have already negatively influenced biota and are predicted to increase (Spangenberg et al. 2009, IPCC 2014, Moore and Olden 2016), which could escalate and expand species loss creating overwhelming conservation situations. Anthropogenic influences can easily disrupt and destroy freshwater biodiversity creating a need for protection and management of remaining populations. If the goal is to protect freshwater faunal biodiversity, then the most critical conservation requirements are those of sensitive species (*e.g. mollusks*).

Mollusk extinction is estimated to be higher than that for all other taxa combined and remaining species are still declining (Strayer 2006, Regnier et al. 2009). Of the mollusks, freshwater mussels (*Bivalvia: Unionidae*) are the most diverse in the United States but over 60% of remaining unionid species are threatened by widespread habitat loss (Williams et al. 1993). The current state of unionid decline in the United States has generated a need for information of environmental variables driving unionid assemblage patterns and distributions. Thus, understanding the distribution and assemblage patterns of mussels and what environmental variables drive them is important in the preservation of all aquatic biodiversity since mussel species are commonly referred to as environmental indicators (Lawler 2003).

A mussel assemblage is a group of species living in the same habitat at the same time. Each assemblage is comprised of several species and their distributions and densities are important to connect subpopulations which help to maintain genetic diversity and metapopulations (Strayer 2008). Local extinction rates have been found to exceed local colonization rates meaning increased habitat fragmentation between subpopulations will leave local assemblages more susceptible to extinction (Vaughn 2012). Defining the distribution and density of assemblages is important in understanding where subpopulations are located for conservation efforts. Unionids are at extreme extinction vulnerability due to their sensitivity to water quality and habitat, complex life cycle involving a specific host fish, long life span, slow growth, and low reproductive rates (Bogan 1993, Strayer et al. 2004, Haag 2012). On account of such complex and numerous life history traits, mussels require a distinctive set of habitat requirements.

An ideal habitat hypothetically needs to provide mussels with low shear stress to allow juveniles to settle, substrate that is soft enough to burrow yet firm enough for support, stream stability that resists constant drought and flood, an environment in which food can be delivered, provides favorable temperatures for growth and reproduction, protection from predators, and has no toxic materials present (Strayer 2008). Also required are the various species of fish hosts vital to provide glochidial dispersal (Watters 1992, Haag and Warren 1998, Vaughn and Taylor 2000). Other environmental factors such as high levels of total suspended solids and inputs of excess sediments have been found to disrupt mussel reproduction and may be drivers of decline (Landis and Stoeckel 2016).

By measuring commonly proposed assemblage drivers such as substrate type, current velocity, water temperatures, water chemistry, and depth (Harman 1972, Allen and Vaughn 2010), we can estimate the drivers of assemblage pattern variations. Assemblage densities and habitat preferences of mussels can be obtained and measured using quantitative quadrat sampling methods (Smith et al. 2003, DeLorme 2011).

There is a lack of comprehensive biotic surveys of freshwater biodiversity and its decline (Lydeard et al. 2004, Darwall and Vie 2005, Higgins et al. 2005, Kuussaari et al. 2009, Regnier et al. 2009, Strayer and Dudgeon 2010). Research has attempted to explain unionid distribution and abundance via single-factor approaches (*e.g.* current velocity, substrate size, etc.), yet these models based upon 1 factor have had little predictive power alone, suggesting that a combination of habitat factors may have more influence on assemblage distribution and abundance (Strayer 2008, Daniel and Brown 2013). Other research has been conducted to examine the relationship between broad scale environmental factors and mussel distributions. These studies have found correlations between landscape features and watershed characteristics with mussel distribution and abundances (Strayer 1983, Strayer 1993, A Di Maio and Corkum 1995, Vaughn 1997, Arbuckle and Downing 2002, Poole and Downing 2004, Gagnon et al. 2006, Daniel and Brown 2013). By implementing a survey to include multiple local habitat variables as well as broad scale factors, a comprehensive and multifactor approach can be used to assess assemblage distribution and abundance. In South Dakota, there is a large gap in unionid research on account of no comprehensive statewide survey or assemblage pattern distribution and density analysis.

Unionids have recently seen a dramatic decline in composition throughout South Dakota (*see Chapter 2)*, which has led researchers to ask fundamental conservation questions. Where are mussels found throughout the state? How dense are the assemblages? What variables are driving mussels to be distributed as they are? A recently completed statewide survey has addressed what species currently inhabit wadable streams in South Dakota and where they are distributed (*see Chapter 2*). The next logical step for unionid conservation in South Dakota is implementing research focused to determine local and broad scale habitat variables driving mussel assemblage density and distribution.

Our research objectives were to quantitatively estimate assemblage densities and evaluate the strength of local versus broad scale drivers in explaining variation in mussel assemblage distribution and abundance throughout South Dakota.

METHODS

Study Area

South Dakota is roughly divided in half by the Missouri River. On the eastern side of the river, land was recently glaciated by the Wisconsin glaciation event (Gewertz and Errington 2015). The Northern Glaciated Plains level IV ecoregion occupies much of the eastern half of the state (USEPA 2013). This region is a continental climate with 510-610 millimeters of annual precipitation and was natively composed of both tall and short grass prairie communities. Today, much of the land has been converted to cultivated agriculture (Auch 2014). The Northwestern Great Plains level IV ecoregion (USEPA 2013) dominates the western side of the state and was not glaciated and is therefore physically different. This region is composed of semiarid rolling plains of shale and sandstone with occasional buttes and badlands. Precipitation is sporadic with 250-510 millimeters falling annually and the landscape is covered by semiarid grassland.

Currently, 15% of the land on the western side of the state is cultivated agriculture (Sayler 2014).

Study Sites

All study sites were located in South Dakota, encompassing 13 major river basins: Bad, Belle Fourche, Big Sioux, Cheyenne, Grand, James, Little Missouri, Minnesota, Missouri, Moreau, Red, Vermillion, and White (Figure 1). A preliminary statewide qualitative survey of 202 sites randomly and proportionately distributed throughout 14 river basins in wadable streams and rivers (surveyed in 2014 and 2015, *see Chapter 2*) revealed 44 sites with live mussel occurrences and these were resampled quantitatively for this study during June and July 2016. These 44 sites were distributed in all basins except for the Niobrara River basin where no live mussels were encountered during our preliminary survey (Figure 1).

For this study, all mussels encountered in the reach sampled at each site were defined as an assemblage. Local habitat variables were those measured within the sampled reach while broad scale habitat variables were those at a water basin or statewide scale.

At each of the 44 sites, assemblage density and habitat parameters were collected using adaptive cluster sampling with 50 initial random start quadrats throughout the reach (DeLorme 2011). Mussels were excavated from a depth of 10 cm from within each quadrat. If live mussels were detected within a quadrat, local habitat variables were collected that included multiparameter sonde measurements (dissolved oxygen percent, dissolved oxygen mgL^{-1}, pH, specific conductance, and water temperature), water depth, and current velocity were all measured 5 cm above the substrate surface from the center of each quadrat. Substrate particle size was measured from 4 random locations within the sample quadrat using a gravelometer and quadrat distance from the left bank was measured to establish channel position.

Broad scale habitat variables measured included level IV ecoregions (USEPA 2013), major river basin geological boundaries, and land area of each of the major river basins were gathered using ArcGIS (10.1/2012, ESRI, California).

Analysis

To estimate which habitat variables had the most influence over unionid assemblage structure in South Dakota, we compiled a database of parameters including local and broad scale habitat affinities. Local habitat variables were averaged from all quadrats at each site. Broad scale environmental variables included the major river basin, level IV ecoregions as defined by USEPA (2013), and basin land area in which each site was located.

Due to a majority of quadrats having no mussel occurrences within our sampling parameters, the data set was reduced by eliminating those species found in <5% of quadrats containing mussels. This allowed for analysis to be focused on only those sites containing species that were present in >5% of the quadrats, which were sites with relatively higher densities of mussels. To validate that the probability that encountering the species found in >5% of quadrats was significantly correlated to the probability of finding the species found in <5% of quadrats, least squares linear regression of mussel densities for each quadrat was conducted in Statistix (10.0/2013, Analytical Software, Tallahassee, FL).

In order to determine how sites were grouped based on habitat variables and densities, we employed a nonmetric multidimensional scaling analysis (NMDS). NMDS is an ordination method based on ranked distances between sites. We used 2 matrices for the mussel assemblage ordination plot. The primary matrix was mussel density averaged from all quadrats at each site and the secondary matrix was the averaged local and broad scale habitat variables for each corresponding site. These 2 matrices were imported into the statistical software PC-ORD (6/2002, MjM Software Design, Gleneden Beach, OR). The distance matrix was constructed by calculating Sørensen (Bray-Curtis) distances. NMDS was then applied to visualize differences among assemblages and relationship of that site arrangement in ordination space to habitat variables overlaid as vectors. Habitat correlations with ordinated sites were used as an evaluation of top environmental drivers of assemblage variation along the axes.

RESULTS

We sampled 2784 quadrats from 44 sites and encountered 11 species, all of which were considered impoundment tolerant (habitat generalist) species (Haag 2012), including 2 that were not encountered in our initial statewide survey (2014-2015, *Chapter 2*), *Lampsilis cardium* (Plain Pocketbook) and *Truncilla donaciformis* (Fawnsfoot) (Table 2). Richness ranged from 0 to 5 with an average of 0.1 species quadrat $^{-1}$ (Figure 2a). Average density was found to be 0.15 mussels m^{-2} and ranged from 0 to 56 mussels m^{-2}

(Figure 2b). Mussels were found in 10 different substrate types, with silt as the most common, comprising 56% of the total substrate samples (Figure 3).

Data reduction to only those species found in >5% of quadrats resulted in 4 remaining species: *Lampsilis siliquoidea* (Fatmucket), *Lasmigona complanata* (White Heelsplitter), *Pyganodon grandis* (Giant Floater), and *Pleurobema sintoxia* (Round Pigtoe) found from 21 sites for the ordination analysis. Regression analysis showed that the probability of encountering those species found in >5% of quadrats was significantly correlated to the probability of encountering those found in <5% of quadrats (F = 20.78, p = <0.001), which suggests that the abundance of these 4 more prevalent species was also a good surrogate for the occurrence of rarer species within the assemblages.

Two ordination axes explained 71% of mussel assemblage distribution with a final 2-dimensional stress of 14.84. Sites were grouped into 4 distinct clusters from the 21 sites analyzed with habitat variables correlated with the 2 axes (Figure 4). The highest local habitat variables correlated most with those axes included silt (r = -0.721), fine gravel (r = 0.718), sand (r = 0.672), and current velocity (r = 0.661) (Table 1). The highest broad scale habitat variables most correlated with those axes were major river basin (r = -0.378) and level IV ecoregion (r = -0.317) (Table 1). Local habitat drivers generally displayed higher correlations with ordination axes than broad habitat drivers.

DISCUSSION

Understanding assemblage densities and environmental drivers influencing assemblage composition can be a powerful tool for conservation and management. Freshwater mussels are naturally patchy in distribution and often aggregated in beds

(Strayer et al. 2004, Strayer 2008), which may give some explanation as to why approximately 92% of our sampled quadrats were void of live mussels. Adaptive cluster sampling was employed in this study as a recommended method for spatially patchy and rare populations (Strayer et al. 2004). Our average assemblage density of 0.15 mussels m^{-2} in South Dakota was found to be roughly comparable to another statewide survey completed throughout 200 sites in Iowa, a state heavily influenced by agriculturally impacted landscapes, in which researchers found the average density to be 0.04 mussels m^{-2} (Arbuckle 2000).

Substrate, current velocity, and conductivity displayed the highest correlations with ordinated species densities. Silt, fine gravel, and sand were highly correlated with assemblage variation, and these fine substrates may be particularly prevalent due to sedimentation input via bank erosion on surrounding terrestrial landscapes (Kronvang et al. 2013). Agricultural landscapes prone to erosion and deposition of fine sediments are also important contributors of dissolved ions resulting in elevated conductivity levels (Dodds and Whiles 2010). These highly modified landscapes also display altered hydrologic response to runoff which in-turn influences seasonal stream flow and velocity patterns within the channel (Peterson 1999).

Sedimentation is the leading cause of biological impairment in North American streams and rivers and is increased as surrounding lands are converted to agriculture, particularly cultivated agriculture (USEPA 2000, Walling and Fang 2003, Collins and Anthony 2008, Collins et al. 2011). In South Dakota, nonpoint source pollution has impaired almost 60% of all assessed rivers and streams with agriculture (grazing or feeding operations) determined as the top pollution contributor (USEPA 2014). Such levels of pollution associated with agriculture usually lead to enhanced sediment loads to stream channels (Box and Mossa 1999, Lummer et al. 2016). In addition to poor agricultural practices, sedimentation can also be a result of benthic disturbances, bank erosion, and hydrological regime changes (Henley et al. 2000, Nobles and Zhang 2011).

Benthic invertebrate distributions are influenced by streambed composition and excess sediments can negatively impact benthic invertebrates in multiple ways (Box and Mossa 1999, Burdon et al. 2013, Lummer et al. 2016). Sedimentation can alter channel morphology and turbidity from suspended fine particles affects primary production by influencing light penetration into the water column, ultimately affecting energy flow and nutrient cycling in a stream (Wood and Armitage 1997, Henley et al. 2000). Fine sediments fill interstitial spaces of the underlying stream substrate, which changes the streambed characteristics and reduces available benthic habitat (Lummer et al. 2016). This sediment alteration leads to a predominance of fine silt, utilized by only the most tolerant habitat generalist mussel species Houp (1993) found a change in mussel assemblage to favor "silt-tolerant" species after 11 years of constant stream sedimentation. Houp's study (1993) also found a shift to increased *P. sintoxia* and *Potamilus alatus* (Pink Heelsplitter), both common species encountered in the 2016 South Dakota survey.

Fish host limitations and geological boundaries have been found to limit the range of mussels (van der Schalie 1945, Schwalb et al. 2012). Each species of freshwater mussel relies on a particular fish host species or multiple fish host species to transport and distribute glochidia (juvenile mussels) throughout the river basin. To investigate whether fish hosts limited the distribution of mussels in South Dakota, all fish host species for each mussel species were identified using an online database (NatureServe 2015). The distribution of each mussel species was then matched to the respective fish host species distribution (fish distribution data obtained from South Dakota State Fish Database, South Dakota State University, Brookings, SD). Each species of mussel and respective fish host(s) were concurrently found in each basin, supporting the conclusion that fish hosts were most likely not limiting freshwater mussel distribution in South Dakota (Table 2).

Level IV ecoregions and river basin boundaries were the top broad scale environmental drivers of our study. This has been found in other research as geological boundaries often limit species distributions throughout a region, which may ultimately influence which species make up an assemblage in a particular area (van der Schalie 1945, Strayer 2008). Ecoregions defined by USEPA (2013) are areas where ecosystems are generally similar, which include type, quality, and quantity of natural resources and are designed to provide a spatial framework for ecosystem monitoring, research, and management. A river basin is the land area that drains all tributaries above a chosen point along a mainstem river (Dodds and Whiles 2010). These may be potential limits on unionid distribution since each river basin is physically disconnected through waterways and each ecoregion has a uniquely different set of ecosystem variables.

Historical geographic disposition of species may also play a role in unionid distribution throughout South Dakota. Unionids are unevenly distributed throughout North America with the top 20 most diverse rivers (except 1) located in the Mississippi River basin (Haag 2012). This reveals that unionids were predisposed to geographical boundary limitations from the beginning of their dispersal throughout North America via recent glaciation events (Near et al. 2001, Elderkin et al. 2008), but little is known about how assemblage distribution and abundance is limited by dispersal (Strayer 2008). The basins found east of the Missouri River had the most abundant and rich assemblages, which may be a result of the recent glaciation. The most recent glacier event in North America receded approximately 10,000 years ago and formed new waterways in which unionids were able to disperse (Clarke et al. 2009). The glacier only extended over eastern South Dakota, thus mussels may have not yet distributed to the western half of the state due to time, hydraulic variability, and/or inadequate habitat factors.

River basin drainage boundary was the top broad scale assemblage driver, suggesting mussel distribution was limited by geographical factors. Studies have strongly agreed that geographical boundaries limit mussel distribution. Unionid range boundaries often end at river basin drainage divides despite adjacent river basins exhibiting similar ecological features (van der Schalie 1945). Such geographical distributions suggest assemblage compositions are dispersal-limited due to river basin boundaries possibly limiting the movement of host fish and predisposed species ranges throughout certain basins from previous glaciation events (Strayer 2008, Schwalb et al. 2011). Distribution limitations are further exemplified in the case of human intervention via breached drainage divides. When the Erie Canal cut through the Alleghenian Divide it linked Lake Erie with waters of the Mohawk River. This linkage resulted in several unionid and fish species rapidly dispersed into the Mohawk River basin in the proceeding decades despite the unfavorable conditions of the canal itself (Strayer et al. 1997, Daniels 2001).

The top 2 broad scale assemblage drivers, major river basin (r=-0.378) and level IV ecoregion (r=-0.317) may play a slight role in assemblage distributions. Mussels throughout South Dakota may be able to survive in adjacent basins, but are just not dispersed there due to geographical limitations of the watershed boundaries. They may have never existed in certain basins since the end of the last glaciation and have not yet dispersed to nearby basins.

In conclusion, average mussel density was 0.15 mussels m^{-2} and the top local habitat assemblage drivers were substrate, current velocity, and conductivity. Fish hosts were suggested not to limit mussel distributions, instead, watershed scale landscape alterations may be possible drivers of existing distribution, densities, and abundance as they influence river and stream sediment composition. All mussel species encountered were habitat generalists, meaning habitat intolerant species have most likely been severely reduced or have vanished entirely throughout the state. It seems as though watershed scale landscape factors are influencing local habitat factors, which in turn, drive assemblage patterns and densities. These results have important management implications for unionid conservation efforts. Future work could include research to examine correspondence in distribution between fish hosts and individual mussel species at finer scales of spatial resolution (sections of major rivers). A more direct assessment of land-use impacts to freshwater mussels is also needed to include differentiation among different tillage and grazing practices. This would facilitate interpretation of broad scale driver influences to freshwater mussel distributions as they exist today.

Table 1. Local habitat affinity correlations of 21 sites in nonmetric multidimensional scaling ordination to each of the 2 axes from adaptive cluster unionid sampling in South Dakota wadeable streams and rivers.

Habitat affinity	r correlation value	
	Axis 1	Axis 2
Temperate (˚C)	-0.252	-0.194
Conductivity (mS cm^{-1}))	-0.416	0.086
Dissolved Oxygen (%)	0.239	0.115
Dissolved Oxygen (mgL^{-1})	0.229	-0.095
pH	-0.031	-0.287
Depth (m)	-0.133	-0.054
Current velocity (m s^{-1})	0.341	0.661
Distance to bank (m)	0.059	0.587
Silt (0.004 - 0.062mm)	-0.140	-0.721
Sand (0.063 - 2mm)	0.169	0.672
Very fine gravel (>2 - 4mm)	-0.238	0.237
Fine gravel (>4 - 8mm)	0.284	0.718
Medium gravel (>8 - 16mm)	0.197	0.549
Course gravel (>16 - 32mm)	0.348	0.320
Very course gravel (>32 - 64mm)	0.224	0.221
Cobble (>64 - 128mm)	0.079	-0.011
Large cobble (>128 – 256mm)	-0.194	-0.125
Boulder (>256 - 512mm)	-0.031	0.063

Table 2. All living unionid species encountered during the 2016 mussel survey of South Dakota with respective host fish and accounts of basin locality of both the mussel species and fish host species. Each mussel species was determined either 'Tolerant' (T) or 'Marginally Tolerant' (M) to impoundments indicated from Haag (2012).

Mussel Species	Mussel Basins	Fish Host	Fish Host Basins
Amblema plicata T	Red	Generalist	All
Elliptio dilatata M	Red	Darters, Sculpins	Big Sioux, Cheyenne, Grand, James, Little Missouri, Minnesota, Missouri, Moreau, Niobrara, Red, Vermillion, White
Pyganodon grandis T	Belle Fourche, Big Sioux, Grand, James, Minnesota, Missouri, Red, Vermillion, White	Generalist	All
Lampsilis siliquoidea T	Big Sioux, Minnesota, Red	Sunfish, Perch, Bluegill, Largemouth bass	All
Lampsilis cardium T	Red	Perch, Sunfish, Banded Killifish, Largemouth bass, Black Crappie	All
Potamilus alatus T	Cheyenne, Missouri, Red	Freshwater Drum	Bad, Belle Fourche, Big Sioux, Cheyenne, Grand, James, Minnesota, Missouri, Red, Vermillion
Pleurobema sintoxia M	Minnesota, Red	Minnows	All
Lasmigona complanata T	Belle Fourche, Big Sioux, Minnesota, Red,	Generalist	All
Leptodea fragilis T	James, Minnesota	Freshwater Drum	Bad, Big Sioux, Belle Fourche, Cheyenne, Grand, James, Minnesota, Missouri, Red, Vermillion
Truncilla donaciformis T	James	Freshwater Drum	Bad, Big Sioux, Belle Fourche, Cheyenne, Grand, James, Minnesota, Missouri, Red, Vermillion
Quadrula quadrula T	James, Red	Catfish	Bad, Belle Fourche, Big Sioux, Cheyenne, Grand, James, Little Missouri, Minnesota, Missouri, Moreau, Niobrara, Vermillion, White

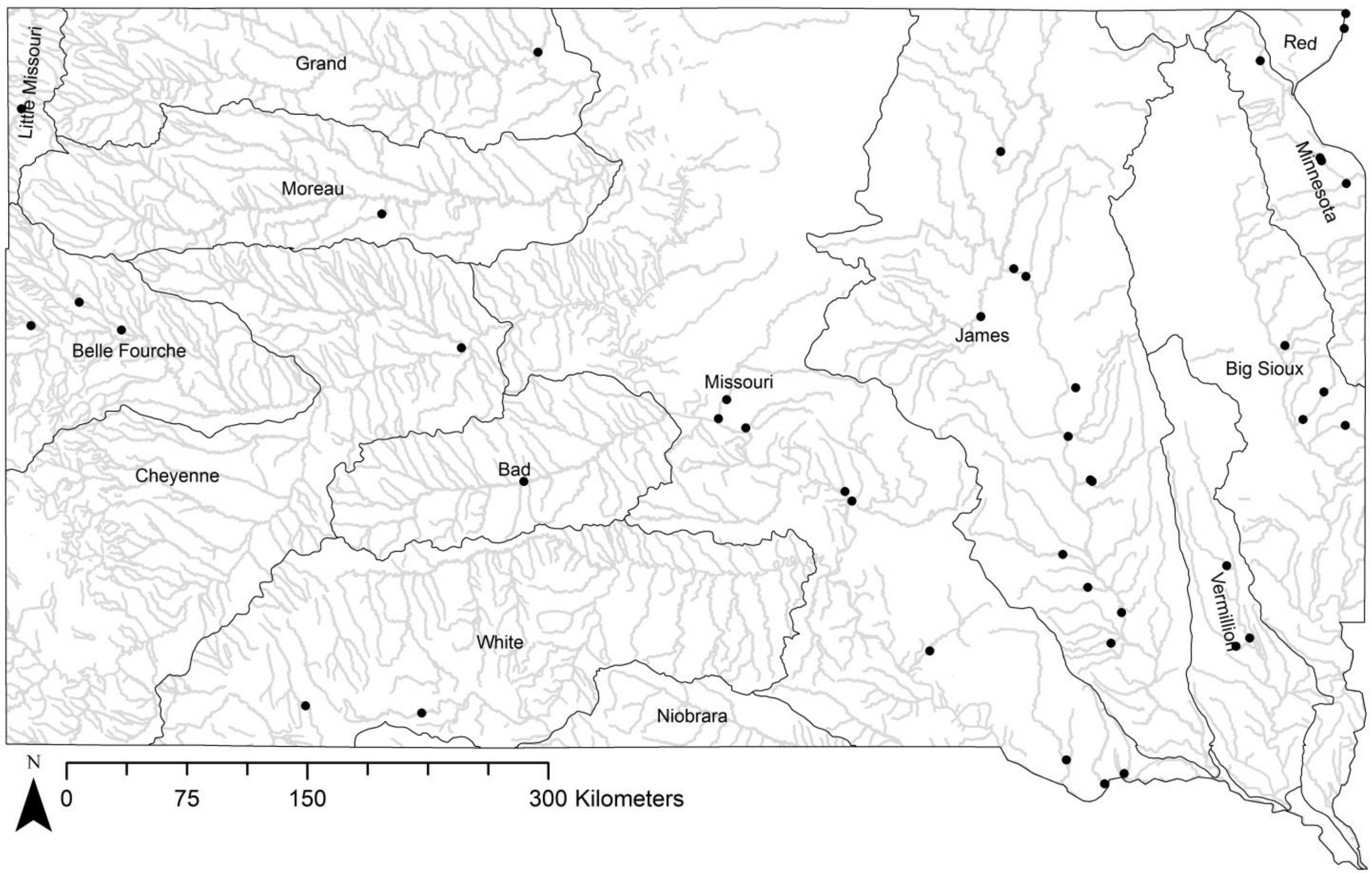
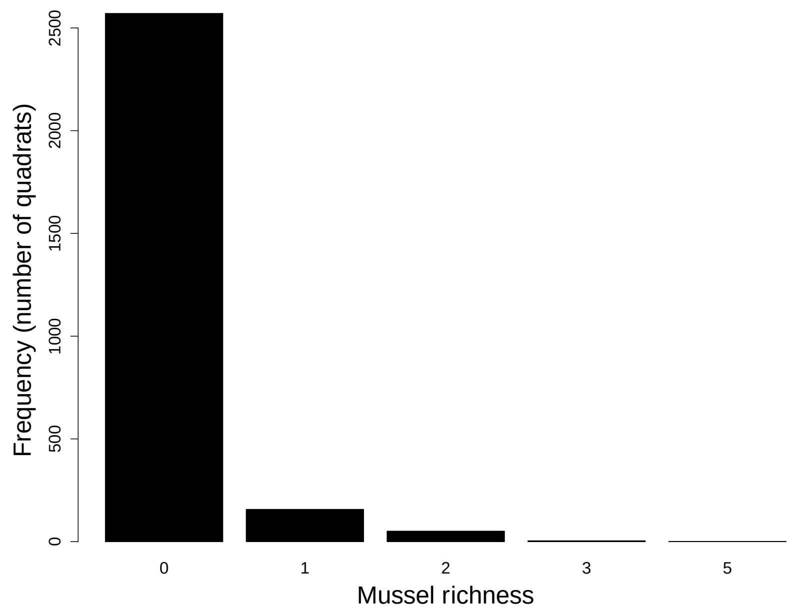


Figure 1. Distribution of sites (n=44) among river basins quantitatively sampled throughout South Dakota in 2016 using the adaptive cluster sampling method (Strayer et al. 2003) to estimate mussel assemblage densities and local and broad scale habitat drivers.

a)



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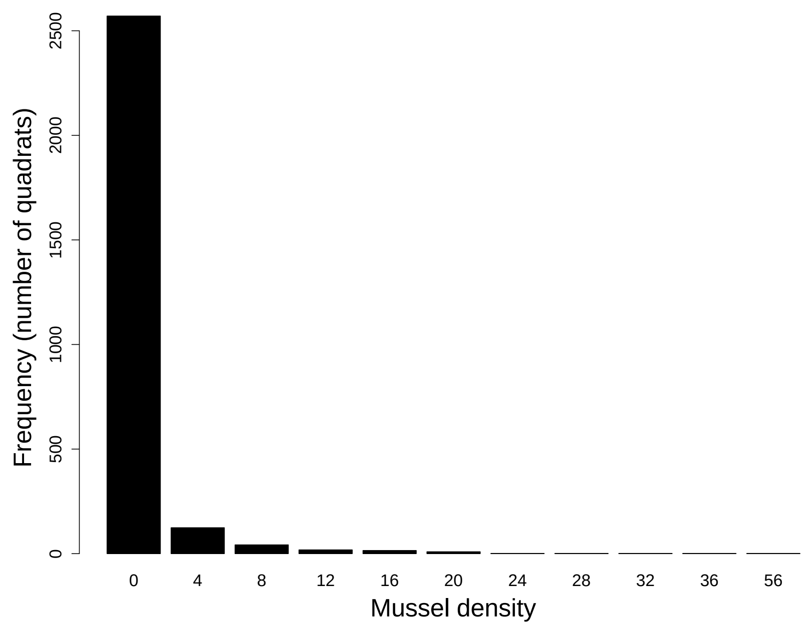


Figure 2. Frequency distribution (number of quadrats) at different magnitudes of a) unionid species richness (mussels m^{-2}) and b) mussel density (mean number m^{-2}).

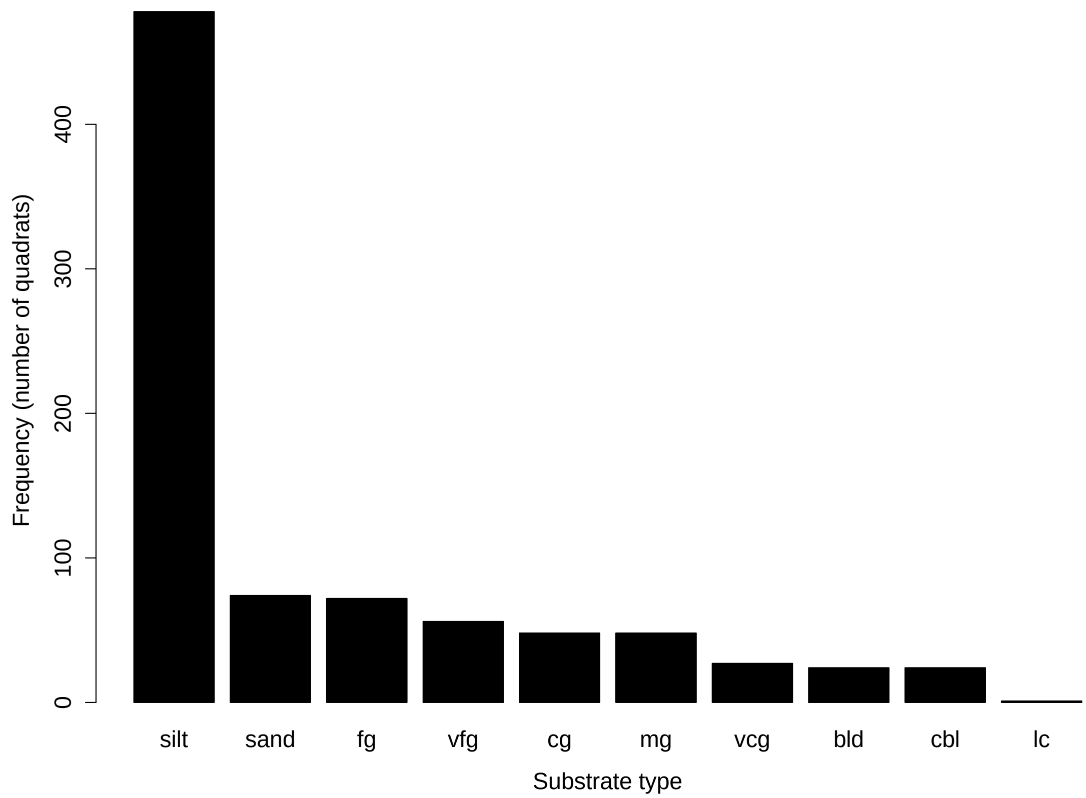


Figure 3. Four random substrate samples taken from each of the 145 quadrats where live mussels were encountered, totaling 580 individul substrate samples during the 2016 quantitative mussel survey in South Dakota. Cummulatively, 10 types of substrate occured: silt (0.004-0.062mm), sand (0.062-2mm), fg = fine gravel (>4-8mm), vfg = very fine gravel (>2-4mm), cg = course gravel (>16-32mm), mg = medium gravel (>8-16mm), vcg = very course gravel (>32-64mm), bld = boulder (>256-512mm), and lc = large cobble (>128-256mm).

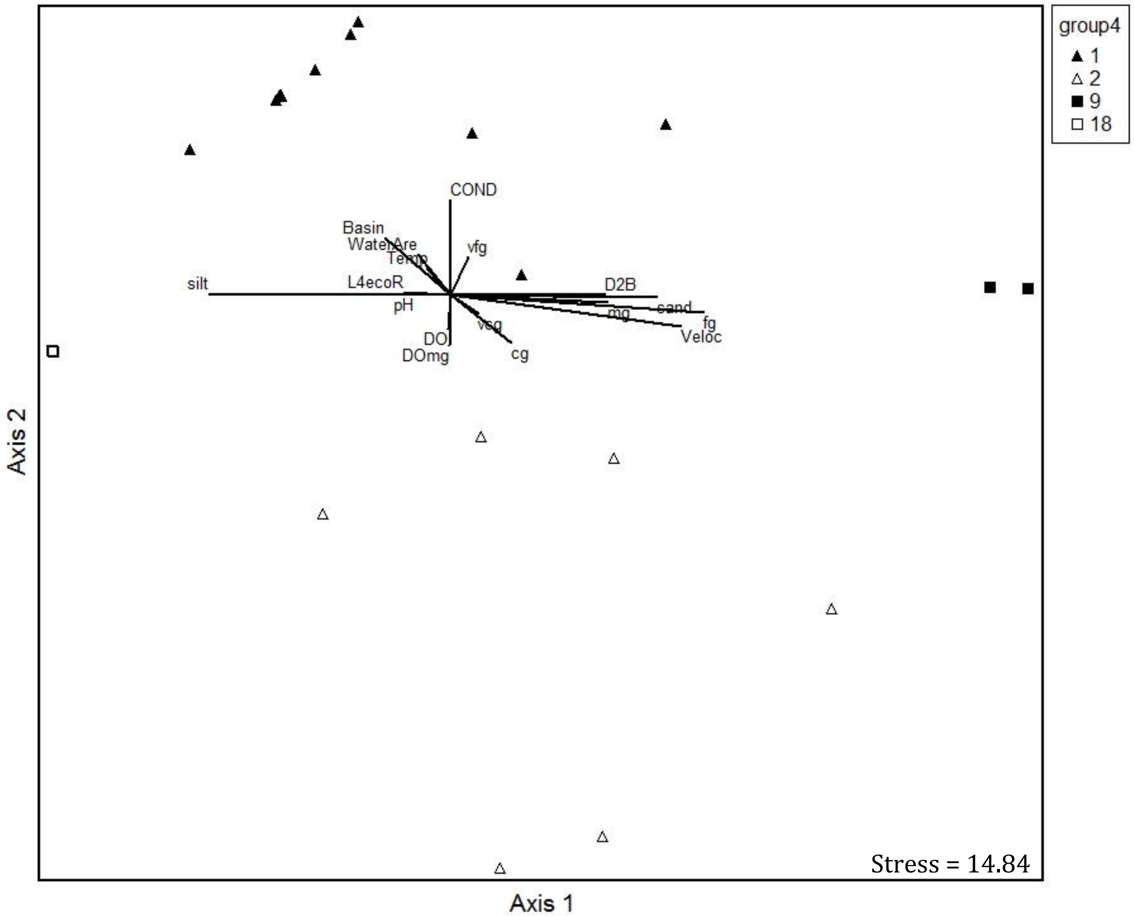


Figure 4. Ordination plot of mussel assemblages at sites only containing species found in >5% of quadrats from 2016 South Dakota survey. Local and broad scale environmental drivers are displayed as vectors correlated with the 2 axes; nonmetric multidimensional scaling based on Sørensen distance, PC-ORD (McCune et al. 2011). The best solution was 2-dimensional (71% of variation among sites, instability = 0.00095). Axis 1 explained the 38% of the variation and axis 2 explained 33% of the variation.

CHAPTER 4: USING QUALITATIVE SURVEYS TO IDENTIFY HOTSPOT AREAS OF UNIONID CONSERVATION IN SOUTH DAKOTA, USA

ABSRACT

Conservation of native freshwater mussel (Family: Unionidae) populations is critical for long-term survival of one of North America's most imperiled groups. This study focused on using qualitative surveys to identify areas of unionid conservation priority throughout South Dakota, USA. Timed searches were conducted at 202 randomly and proportionally distributed sites throughout wadable, perennial streams rivers in 14 major river basins in South Dakota. Evidence of mussels was found from 78 sites (39%) and each site was ranked into 1 of 4 conservation priority categories ('none', 'low', 'medium', or 'high') based upon diversity, richness, individual abundance per species, and relative abundance of species of a critical or listed status. Seventy four percent of sites were located in eastern South Dakota with 67% of 'high' priority sites located in the Minnesota River basin. Overall, the James River basin had the greatest number of ranked sites (30%) followed by the Big Sioux basin (17%). Based on our results, conservation efforts could include protecting current populations and possibly expanding the distributions through species re-introductions. These efforts may be most effective if focused in eastern basins, particularly in the James, Minnesota, and Big Sioux River basins, most of which were included in preexisting aquatic Conservation Opportunity Areas by South Dakota Fish, Game & Parks.

INTRODUCTION

In an era of increasing worldwide biodiversity decline, conservation of remaining species is crucial for highly imperiled faunas, especially in freshwater ecosystems (Master et al. 2000, Dirzo and Raven 2003, Dudgeon et al. 2006). Despite occupying <1% of Earth's surface, freshwater systems have already lost approximately 20% of species to extinction (Abramovitz 1996, Strayer and Dudgeon 2010). Conservation efforts are usually focused towards keystone species, which are typically dominated by plant and vertebrate groups. Yet studies have found that invertebrates can be strong predictors of conservation priority for vertebrates, but not vice versa (Moritz et al. 2001). Invertebrates represent approximately 99% of faunal diversity, yet worldwide invertebrate-focused conservation efforts are lacking (Bouchet et al. 1999, Meyers 2000).

The freshwater mollusk group of invertebrates are highly imperiled, making up nearly 40% of all known animal extinctions, yet mollusk conservation is commonly disregarded (Bouchet et al. 1999). One of the most threatened groups of mollusk in North America is native freshwater mussels (Family: Unionidae) with approximately 55% of these species extinct or imperiled (Williams et al. 1993, Master et al. 2000).

The root of mussel decline stems from habitat degradation, which is largely influenced by anthropogenic alterations of land (*ie*. agriculture) that disrupts stream and river systems (Williams et al. 1993, Strayer and Dudgeon 2010, Haag et al. 2012, Daniel and Brown 2013). Land is heavily altered in certain parts of North America, particularly in the U.S. Corn Belt region where landowners are increasing conversion of grasslands to cultivated crop fields to aid the growing demands of biofuels and food (Johnston 2013, Wright and Wimberly 2013). In South Dakota, row crops comprise approximately 57%

of land east of the Missouri River and approximately 9% of land west of the river (ArcMap 10.1/2012, ESRI, California). The USEPA (2014) has determined that nonpoint source runoff in South Dakota has impaired 60% of all assessed streams and rivers. As crop management pressure continues to result in the conversion of more land throughout the state, conservation of imperiled aquatic species becomes critical for the future of aquatic biodiversity.

Unionids are considered an umbrella species for many other aquatic invertebrates because they are highly sensitive to changes in aquatic environments, relatively sedentary, highly imperiled, and long-lived (Geist 2010). Thus defining areas of conservation priority for mussels will most likely have positive impacts on other freshwater fauna. Within the past 100 years, South Dakota has seen a potential decline from 36 to 15 mussel species (*see Chapter 2*) which has created a need to identify areas that would be most effective for conservation as a base for establishing a conservation plan.

The objective for this research was to identify areas of top conservation priority in South Dakota by ranking randomly surveyed sites (n = 202) into 1 of 4 conservation priority categories defined by McRae et al. (2004).

METHODS

Site Selection

A statewide freshwater mussel survey was executed during the summers of 2014 and 2015. A total of 202 sites were randomly generated among wadable, perennial mainstream, and tributary streams throughout 14 major river basins in South Dakota using ArcMap (10.1/2012, Esri, California) (Figure 1a). Major river systems included the

Bad, Belle Fourche, Big Sioux, Cheyenne, Grand, James, Little Missouri, Minnesota, Missouri, Moreau, Niobrara, Red, Vermillion, and White (Figure 1a). East of the Missouri River, 102 sites were randomly and proportionately generated based upon watershed area and the same process repeated for the 100 sites allocated west of the Missouri River. Each randomly generated point was re-established to the closest perennial stream within the appropriate basin with the exception of the 7 resurvey sites that were selected based upon historical surveys (1975-2005), landowner permissions, and accessibility, thus not considered random (Figure 1a). Sites where landowner permission could not be obtained or where there was a lack of flowing water were replaced with another random stream within the same river basin.

Mussel Surveys

Sites east of the Missouri River were surveyed from 4 June to 14 August 2014, while those west of the Missouri River were surveyed from 27 May to 27 July 2015. Timed, qualitative searches were employed to survey mussel occurrence and species composition following the wadable rivers protocol of DeLorme (2011). Each site (n = 202) was visited and searched for 2 person-hours starting from the nearest access point and moving in an upstream direction. All living mussels, empty shells, and shell fragments detected by visual and tactile means were collected for identification and live mussels were measured for length, width, depth, and photographed for documentation. Supplemental searching via snorkeling was used in deeper water but within the allotted search time. Those specimens difficult to identify in the field were returned to the laboratory for further identification. Mussels not kept for identification or vouchers for the South Dakota Aquatic Invertebrate Collection at South Dakota State University, Brookings, SD, were returned to the stream.

Analysis

Distribution, species richness, and abundance were determined and totaled using ArcMap (Version 10.1/2012, ESRI, California) and Microsoft Excel (14.1.0/2011, Microsoft Corporation). Species richness was determined as the sum of all species represented by empty shells and live specimens for the area of interest. Abundance was determined as the sum of all empty shells and live specimens for the given area of interest. Diversity was calculated using the Shannon-Wiener Diversity Index (Krebs 2009):

$$H' = -\Sigma p_i \ln(p_i),$$

where 'p_i' is the proportion of individuals in the 'ith' species and 'ln 'is the natural logarithm. Differences in assemblages between eastern and western sides of the state were calculated with a 2-sample t-test in Statistix (10.0/2013, Analytical Software, Tallahassee, FL).

All sites with occurrences of living mussels and whole shells were included in this analysis. We followed the ranking protocol defined by McRae et al. (2004) with a slight modification to the criteria regarding intolerable species. McRae et al. (2004) used relative abundance of intolerant individuals (RAIU) where they identified species tolerance according to the type of habitat and substrate preferred by the species of interest. Since their method was cursory, not clearly defined, and no work has been published defining each unionid species specific tolerance value, we used relative abundance of species that are of a critical or listed status (RALU) for South Dakota defined in Williams et al. (1993).

Each sites (n = 202) from our statewide survey showing evidence of mussels was ranked into 1 of 4 categories to determine conservation priority (Table 1).

RESULTS

Mussel Survey

We collected 1151.5 individuals of 15 species from 91 sites within 14 river basins in South Dakota. The remaining 111 sites had no evidence of mussels. Two dominant species accounted for 73% of total abundance among all species: *Pyganodon grandis* (Giant Floater) (63%) and *Lasmigona complanata* (White Heelsplitter) (10%). Significant differences were found in assemblage composition between basins east and west of the Missouri River. Species richness ranged from 0 - 7 per site in basins east of the Missouri River, which was significantly greater (t = 5.81, p = <0.001) than richness observed from basins located west of the Missouri River (0 - 2 species per site). Abundance was also significantly higher in eastern South Dakota than abundance observed from western basins (t = 3.84, p = <0.001), as was diversity (t = 4.67, p = <0.001).

Site Ranking

Of the 91 sites with evidence of mussels, 13 had only shell fragments and were ranked as ‘none’, meaning they take no conservation priority. The remaining 78 sites were ranked for conservation priority. We found 3 sites ranked as ‘high’ conservation priority, 10 as ‘medium’, and 65 as ‘low’ priority (Table 2). Seventy-four percent of ranked sites (n = 58) were located east of the Missouri River and the remaining 26% (n = 20) were located in basins west of the Missouri River (Figure 1b). Basins in eastern South Dakota included all 3 ‘high’ priority, 9 ‘medium’ priority, and 46 ‘low’ priority sites. Western basins included 1 ‘medium’ priority and 19 ‘low’ priority sites (Table 2).

The James basin contained the greatest number of ranked sites (n = 23 or 30%), including 1 ‘high’ ranked site, followed by the Big Sioux basin with 13 ranked sites (17%). The Minnesota River basin included 2 ‘high’ priority sites, which represented 50% of sites from this basin and 67% of ‘high’ priority sites.

DISSCUSSION

Despite the presumed accumulation of threats to waterways in South Dakota and the recent decline of statewide unionid species richness, South Dakota still remains habitat for a few impoundment tolerant (habitat generalist) species (Haag 2012) such as *P. grandis*, *L. complanata*, and *Pleurobema sintoxia* (Round Pigtoe) that appear to be abundant throughout the state, but in low average densities of 0.15 m^{-2} (*see Chapter 3*). The significant spatial patterns between basins east and west of the Missouri River suggests that eastern basins may have more favorable habitat conditions and fewer environmental stressors to the remaining species currently inhabiting the area. This is not surprising as eastern and western halves of South Dakota have noticeably different glacial histories and ecosystem properties.

The eastern half includes the prairie pothole region that was created by the latest Pleistocene (Wisconsin) glaciation event. Unionid distribution was influenced by glacial meltwaters that facilitated redistribution and colonization upstream from southern habitats as river confluences allowed mussels to distribute throughout watersheds (Graf 1997). Western South Dakota is unglaciated, thus mussels have most likely established this region through the Missouri River drainage as a dispersal corridor. Streams throughout eastern South Dakota are more hydrologically stable than those in the western half. Streams within western basins are highly prone to intermittency and flash flooding that disturbs substrates creating conditions of highly variable total suspended solids concentrations (Hoke 2011). Mussels need a unique habitat requirements including substrate that is soft enough for burrowing yet firm enough to provide support and a stable current velocity that allows nutrients and food to be delivered and not prone to flooding/drying events that could result in filling and scouring of the stream bed (Strayer 2008).

Based on our analysis unionid conservation efforts would most likely be most effective in areas with multiple ‘high’ and ‘medium’ ranked sites, which were mainly located east of the Missouri River, particularly in the Big Sioux, James, and Minnesota River basins where we found multiple areas of high unionid diversity. These 3 basins contained all ‘high’ priority sites and represented the most sites assigned a priority ranking. Particular conservation focus may be given to the Whetstone River in Roberts and Grant Counties, Medary Creek and Six Mile Creek in Brookings County, Bios de Sioux River in Roberts County, Split Rock Creek in Minnehaha County, Shue Creek in Beadle County, Lone Branch Creek in Hutchinson County, Cottonwood Creek in Jackson County, and the James River in Hanson County. Mussel conservation efforts focused in these areas will likely result in improved mussel habitat and prolonged conservation of the remaining established populations.

All 'high' priority sites and most 'medium' priority sites overlapped with South Dakota Fish, Game, & Parks Aquatic Conservation Opportunity Areas (Figure 1b) (SDFGP 2014). Conservation Opportunity Areas identify landscapes that represent the most diverse aquatic habitats in order to maximize the limited resources devoted to conservation while providing the most direct benefits to aquatic ecosystems. These areas were based on 3 criteria: highest confirmed/probable species richness, lowest human stressor index value, and highest percentage of public ownership (SDFGP 2014). The Conservation Opportunity Areas provide South Dakota resource managers with a framework of areas for consideration of increased conservation, management, enhancement, and protection emphasis. The locations of most sites for unionid conservation priority were found to be included in the Conservation Opportunity Areas.

Developing practical and sustainable conservation strategies for imperiled fauna requires cost consideration, conservation objectives, conservation strategies, predictions, and unavoidable tradeoffs. Unionid conservation needs to focus on persistence of the species over time, maintenance of genetic variability, and ensuring that habitat does not further degrade, all while minimizing management costs. To begin creating a management plan, spatial scale of the management area needs to be determined by resource managers, which range from an individual assemblage level to an entire river basin or even at a statewide scale. The goals of conservation also need to be determined by resource managers before implementing any conservation strategies. Goals could include protection and maintenance of remaining viable populations, expanding a population, and/or maintaining genetic diversity (Geist 2010, Smith et al. 2015).

After conservation scale and management goals are established, appropriate strategies can be implemented. There are many perceivable strategies for conservation management including, restoration, augmentation, reintroduction, regulations and easements, and public outreach. Restoration implies returning population numbers to a status determined by historical levels. Since this was the first statewide survey for South Dakota (*see Chapter 2*), obtaining historic abundance levels for every basin, stream, and river may be near impossible. Augmentation would mean releasing previously propagated individuals into a stream in which that species currently exists, provided the habitat is still suitable. This strategy was found to be effective when applied at a small spatial scale to a population within a stream in North Carolina (Smith et al. 2015). Reintroduction would be most productive if the habitat requirements were sufficient and stable. If the goal would be to expand a current viable population, addition of new individuals to that population would not only likely increase the abundance but the genetic diversity as well. Laws restricting management practices within the watershed would be logistically challenging to create or change, but efforts to increase existing easements may be more feasible. Current easements already in place in South Dakota that can increase acreage in buffer zones on lands adjacent to streams or increase the area of native vegetation within a watershed, both of which would hypothetically help mussel habitat. Public outreach is another important component to most conservation. Without the support of the public, conservation actions would not be as easily applied and no support could be a limitation on action.

Smith et al. (2015) modeled many different forms of conservation strategies while taking into account limits in funding and included tradeoffs (conservation benefits versus management cost and relative importance of persistence) to assess best conservation strategies of an endangered species, *Alasmidonta heterodon* (Dwarf Wedgemussel), in North Carolina. Their model found the most promising strategy was to either focus on persistence and protection of current populations in a major river basin or apply a balanced approach involving protection of the current populations with attempts to expand their distribution. Persistence of a population largely would rely on protection and improvement of typical habitats (Smith et al. 2015). Again, this study was modeled on a single, highly rare, and endangered mussel species and does not necessarily imply the same outcome for other geographical areas.

In South Dakota, we know the distributions and abundance of extant mussel assemblages (*see Chapter 2*) in which we have determined hotspots of the highest diversity for conservation. While some predictions or assessments of habitat requirements in recently vacated streams need to be made, protecting the hotspot areas and possibly attempting to expand the distribution within the stream or river may be the first step. Of course, resource managers need to determine the goals of conservation, but the data presented in Chapters 2 - 4 of this thesis provides a baseline for discussion of management options.

Table 1. Criteria for defining the conservation priority of the unionid survey sites (n = 202) in South Dakota based upon McRae et al. (2004). " 'H' " represents the Shannon-Wiener Diversity Index (Krebs 2009) and "RALU" is the relative abundance of species that are of critical or listed status in South Dakota (Williams et al. 1993).

Site rank	Criteria
None	No living mussels
Low	1 – 3 species present
	$0 < H' \leq 0.35$
	RALU = 0
Medium	4 – 8 species present
	$0.35 < H' \leq 0.65$
	$0 <$ RALU ≤ 0.10
High	> 8 species present
	$H' > 0.65$
	RALU > 0.10

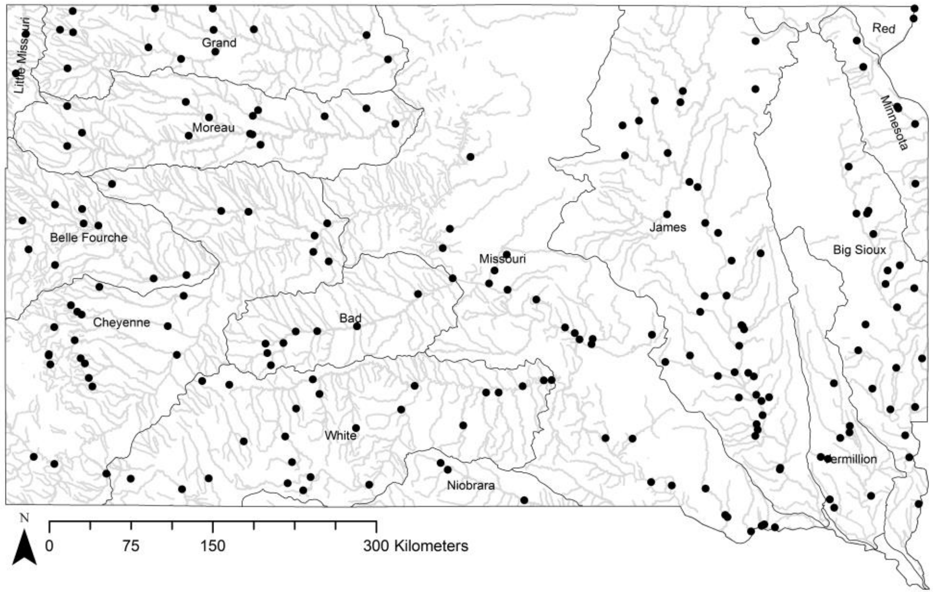
Table 2. Sites (*n* = 78) from a statewide unionid mussel survey ranked into 3 conservation priority categories where ‘H’ indicates Shannon-Weiner Diversity Index, ‘$\bar{x}$ ind/sp.’ indicates the mean individuals per species, and ‘RAIU’ represents relative abundance of species of special concern.

Site ID	Basin	Abundance	Richness	H'	$\bar{x}$ ind/sp.	RALU	RANK
122543556	Minnesota	98	4	0.800	24.5	0	HIGH
125118403	James	76	3	0.654	25.333	0	HIGH
122543582	Minnesota	66.5	4	1.193	16.625	0	HIGH
126201408	Red	64	7	1.608	9.143	0	MEDIUM
126723736	Big Sioux	56.5	4	0.633	14.125	0	MEDIUM
126201265	Red	36.5	7	1.783	5.214	0	MEDIUM
122544791	Minnesota	31.5	4	1.197	7.875	0	MEDIUM
145664464	James	29	4	1.123	7.250	0	MEDIUM
126752089	Big Sioux	17	3	0.578	5.667	0	MEDIUM
125122403	James	15.5	3	0.380	5.167	0	MEDIUM
128608934	Bad	13	2	0.429	6.5	0	MEDIUM
130991546	Big Sioux	6.5	5	1.378	1.3	0.077	MEDIUM
125121736	James	5.5	5	1.516	1.1	0.091	MEDIUM
142193204	James	119.5	3	0.559	39.833	0	LOW
145664423	James	64	3	0.313	21.333	0	LOW
125120762	James	54.5	1	0	54.5	0	LOW
128622793	Bad	39	1	0	39	0	LOW
123213075	Vermillion	32.5	3	0.274	10.833	0	LOW
154853605	Belle Fouche	27.5	2	0.567	13.75	0	LOW
148154318	Missouri	20	1	0	20	0	LOW
125119340	James	20	2	0.199	10	0	LOW
144108417	Missouri	19	2	0.515	9.5	0	LOW
123214549	Vermillion	18.5	2	0.675	9.25	0	LOW
148186336	Missouri	17	1	0	17	0	LOW
154887379	Belle Fouche	15	1	0	15	0	LOW
123214782	Vermillion	12.5	6	1.506	2.083	0	LOW
128457345	Missouri	10	2	0.325	5	0	LOW
145659649	James	8.5	1	0	8.5	0	LOW
122530954	Minnesota	8	1	0	8	0	LOW
145659638	James	7	1	0	7	0	LOW
134297609	Little Missouri	7	2	0.410	3.5	0	LOW
128463882	Missouri	6	2	1.011	2	0	LOW
128461849	Missouri	6	1	0	6	0	LOW
126558815	White	6	1	0	6	0	LOW
130957122	Big Sioux	5.5	1	0	5.5	0	LOW
156015785	Cheyenne	5.5	1	0	5.5	0	LOW
148610405	James	5	1	0	5	0	LOW
145664785	James	5	2	0.500	2.5	0	LOW
148182229	Missouri	5	1	0	5	0	LOW
154730365	White	5	1	0	5	0	LOW
130961436	Big Sioux	4.5	1	0	4.5	0	LOW

(Table 2 continued)

125114454	James	4.5	1	0	4.5	0	LOW
148605589	James	4.5	1	0	4.5	0	LOW
126756632	Big Sioux	4	1	0	4	0	LOW
126727977	Big Sioux	4	3	1.040	1.333	0	LOW
145664664	James	4	1	0	4	0	LOW
123209041	Vermillion	4	2	0.693	2	0	LOW
145664782	James	4	3	1.040	1.333	0	LOW
151660862	Moreau	4	1	0	4	0	LOW
151672610	Moreau	4	1	0	4	0	LOW
151672479	Moreau	4	1	0	4	0	LOW
126723781	Big Sioux	3	2	0.637	1.5	0	LOW
154730348	White	3	1	0	3	0	LOW
154879187	Belle Fouche	2.5	2	0.500	1.25	0	LOW
126740053	Big Sioux	2	1	0	2	0	LOW
125108393	James	2	1	0	2	0	LOW
145664811	James	2	2	0.693	1	0	LOW
148176241	Missouri	2	2	0.693	1	0	LOW
128460016	Missouri	2	1	0	2	0	LOW
143214747	Grand	2	2	0.693	1	0	LOW
145660337	James	1.5	2	0.637	0.75	0	LOW
125119006	James	1.5	1	0	1.5	0	LOW
144249212	James	1.5	1	0	1.5	0	LOW
130957023	Big Sioux	1.5	1	0	1.5	0	LOW
126728122	Big Sioux	1	1	0	1	0	LOW
126725959	Big Sioux	1	1	0	1	0	LOW
125127308	James	1	1	0	1	0	LOW
128456968	Missouri	1	1	0	1	0	LOW
148182065	Missouri	1	1	0	1	0	LOW
128629116	Bad	1	1	0	1	0	LOW
150347613	Cheyenne	1	1	0	1	0	LOW
143179857	Grand	1	1	0	1	0	LOW
149713796	Niobrara	1	1	0	1	0	LOW
144259482	Missouri	0.5	1	0	0.5	0	LOW
125115300	James	0.5	1	0	0.5	0	LOW
130956900	Big Sioux	0.5	1	0	0.5	0	LOW
150336685	Cheyenne	0.5	1	0	0.5	0	LOW
143180537	Grand	0.5	1	0	0.5	0	LOW

(a)



(b)

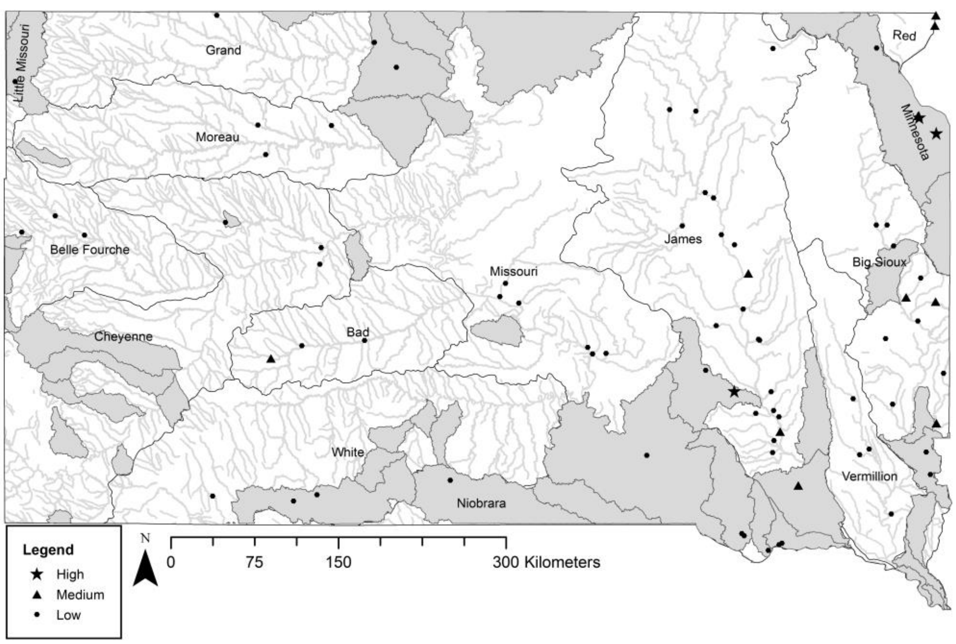


Figure 1. South Dakota study area depicting (a) mussel survey site locations (n = 202) throughout the 14 labeled major river basins of South Dakota and (b) the location of the 78 sites and their respective conservation priority ranking. The gray shaded areas are Conservation Opportunity Areas determined by South Dakota Fish, Game, & Parks.

CHAPTER 5: THESIS CONCLUSIONS

The first objective of this study was to document the current distribution, species composition, and abundance of native freshwater mussels, and to assess unionid decline relative to historical accounts. Throughout the 202-site qualitative comprehensive statewide survey we encountered 15 species, 11 represented by live specimens. All 15 were encountered east of the Missouri Rivers and 5 were encountered west of the Missouri River. The most abundant species was *Pyganodon grandis* (Giant Floater), which represented 63% of all mussels found. Remaining species each represented no more that 10% of total abundance. Habitat and host fish generalists (Haag 2012), *P. grandis* and *Lasmigona complanata* (White Heelsplitter), typically dominated the assemblages by comprising of 73% of the total abundance. Live specimens of *Elliptio dilatata* (Spike) were found, as well as a single valve of *Venustaconcha ellipsiformis* (Ellipse), both species had not been encountered in South Dakota and are thus new state records. Results concluded that species were unevenly distributed throughout the state with the large majority of the species and abundance found in basins east of the Missouri River.

To assess species decline, we resurveyed 7 sites from historical accounts and found evidence of an average decline in species richness of 1 species per 10 years. A species richness decline of 58% was determined from combined richness of 15 historic surveys (1915-2005) compared to our comprehensive statewide survey (2014-2015). Basin-wide comparisons from 11 historic surveys (1975-2005) to our survey found evidence of a 50% decline in species richness. Of the historical 36 species that existed in South Dakota from 1915-2005, 7 species were found to comprise 73% of the total abundance among mussel species. We encountered 15 total species with only 2 species comprising 73% of total abundance among all species indicating a recent shift to habitat generalist species (Haag 2012). Objective I conclusions support a recent statewide species decline and a shift to species generalist-dominated assemblages with the majority of the species and abundance occurring in eastern South Dakota.

The second objectives of this research were to estimate assemblage density and identify critical environmental drivers that explain significant variation among mussel assemblages in South Dakota. We quantitatively sampled 44 sites with adaptive cluster sampling to estimate local and broad scale habitat variables driving assemblage variation and mussel assemblage density. These 44 sites were chosen based on the initial 202 site, qualitative survey in which live mussels were found. In visiting these sites, we encountered 2 different species not encountered in the previous survey, bringing the total to 17 species statewide. Average density was found to be 0.15 mussels m^{-2} with 0 to 56 individuals m^{-2}. Nonmetric multidimensional scaling analysis revealed silt ($r = -0.721$), fine gravel ($r = 0.718$), sand ($r = 0.672$), conductivity ($r = -0.416$), and current velocity ($r = 0.661$) as the highest local variables most correlated with the ordination axes ($n = 2$), and were found to be the top local habitat drivers of assemblage variation. Top broad scale drivers were found to be major river basin boundaries ($r = -0.378$) and level IV ecoregion ($r = -0.317$). Fish host species were found not to limit mussel distributions since each species of mussel and respective fish host(s) were concurrently found in each basin. Mussel distributions may be influenced by excess inputs of water pollution, which has been determined to impair 60% of all assessed rivers and streams in South Dakota (USEPA 2014). Species most often occurred in silt substrate (56%), suggesting that at least some mussel species are able to tolerate the degraded stream habitat conditions found in South Dakota.

The third and final objective was to determine areas of unionid conservation priority across the state. Three sites were found to be of high priority, 10 of medium priority, and 65 of low priority by our calculations based on McRae et al. (2004). Unionid conservation efforts would be most effective in areas with multiple 'high' and 'medium' ranked sites, which were mainly located east of the Missouri River, particularly in the Big Sioux, James, and Minnesota River basins where we found multiple areas of high unionid diversity. These 3 basins contained all 'high' priority sites, and represented the most sites given a conservation priority ranking. Particular conservation focus may be given to the Whetstone River in Roberts and Grant counties, Medary and Six Mile Creeks in Brookings County, Bios de Sioux River in Roberts County, Split Rock Creek in Minnehaha County, Shue Creek in Beadle County, Lone Branch Creek in Hutchinson County, Cottonwood Creek in Jackson County, and the James River in Hanson County. Conservation efforts focused in priority areas of unionid species will likely result in improved mussel habitat and prolonged conservation of remaining species. All of the 'high' priority sites and most of the 'medium' priority sites overlapped aquatic Conservation Opportunity Areas defined by South Dakota Fish, Game & Parks SDFG&P 2014). These areas are key landscapes for potential management, conservation, and protection.

Overall, this study found evidence of 17 species statewide. It is apparent that native freshwater mussels are declining in South Dakota and assemblages have shifted to impoundment tolerant species, lowering the diversity of unionids. Although multiple environmental components structure mussel distribution (Ries et al. 2016), local habitat variables (substrate, current velocity, and conductivity) played a significant role in driving assemblage variation in South Dakota. Broad scale environmental factors also influence mussel distributions through regional patterns in land use, human population density and natural landscape features. A majority of South Dakota's land is used for agricultural practices, which increases the amount of nonpoint source pollution and sediments into streams and rivers- the top pollutant in streams nationwide (Naimo 1995, Richer et al. 1997, Haag 2012). Mussels are environmentally sensitive species and can be negatively affected by increased amounts of sediments and landscape alterations on terrestrial lands adjacent to the stream or river (Richer et al. 1997).

While more research would benefit the understanding of broad scale watershed characteristics associated impacts on mussel habitat requirements, successful conservation in highly impacted agricultural watersheds must take into consideration the intimate and complex connection between aquatic and terrestrial ecosystems.

Our data will provide management agencies with baseline distribution, abundance, and mussel assemblage data, which will aid future generations partaking in unionid surveys in detecting any changes in mussel assemblages over time. Many mussel species still exist throughout South Dakota and could benefit from a long-term survey and monitoring program to assess the distribution, abundance, recruitment, and biological status. A long-term monitoring plan should consist of surveying a set of sites over a decided period of time in the same manner as presented in this thesis for comparison purposes. These sites should be a spatially explicit subset of sites with high mussel abundance and richness, which would allow for resource mangers to focus efforts at a suitable location and scale. Other recommendations would be to maintain unionid habitat integrity, preserve remaining populations with possible range expansion through introductions, enact further research of wide-scale watershed impacts on freshwater streams and mussels, and to establish a protection management goal for South Dakota that would contribute toward national recovery and sustainment efforts of freshwater native mussels.

This research provided a foundation for future unionid research in South Dakota. Additional studies examining fish host distributions in accordance with mussel species localities and watershed-scale environmental impacts on streams would be useful to improve our understanding of the effects directly impacting mussel habitats and thus, assemblage distributions. Further beneficial studies would include investigation of deep water (non-wadable) rivers and lakes that we were unable to sample during this study as well as research on the spread of the invasive *Dreissena polymorpha* (*zebra mussel*), into South Dakota and their potential impacts on unionids.

APPENDIX I

Individual distribution maps for all 15 species found throughout the 202 site survey of wadable streams and rivers in South Dakota during the years 2014 and 2015.

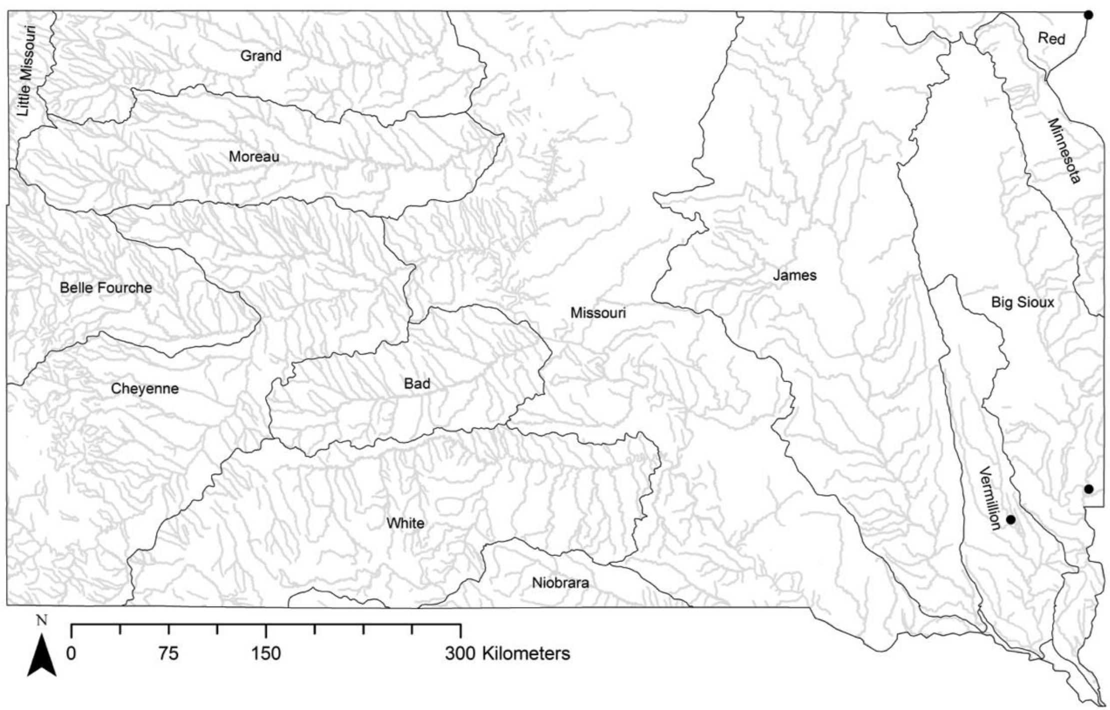


Figure 1: Distribution of *Amblema plicata* from the 2014-2015 statewide survey.

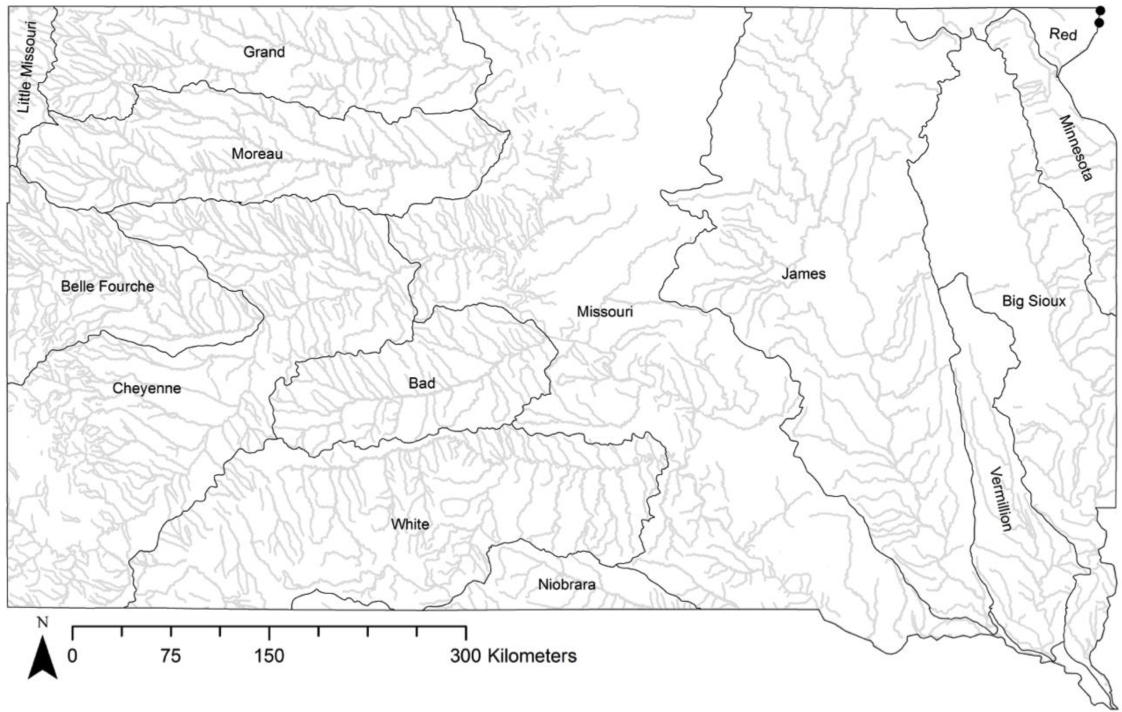


Figure 2: Distribution of *Elliptio dilatata* from the 2014-2015 statewide survey.

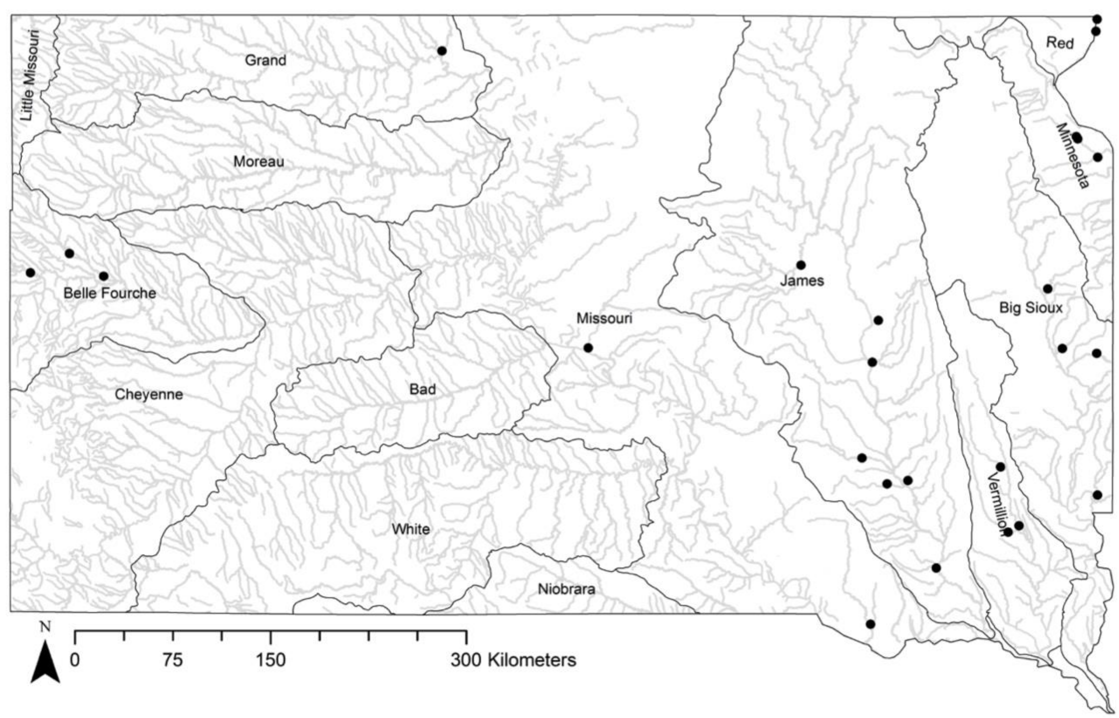


Figure 3: Distribution of *Lasmigona complanata* from the 2014-2015 statewide survey.

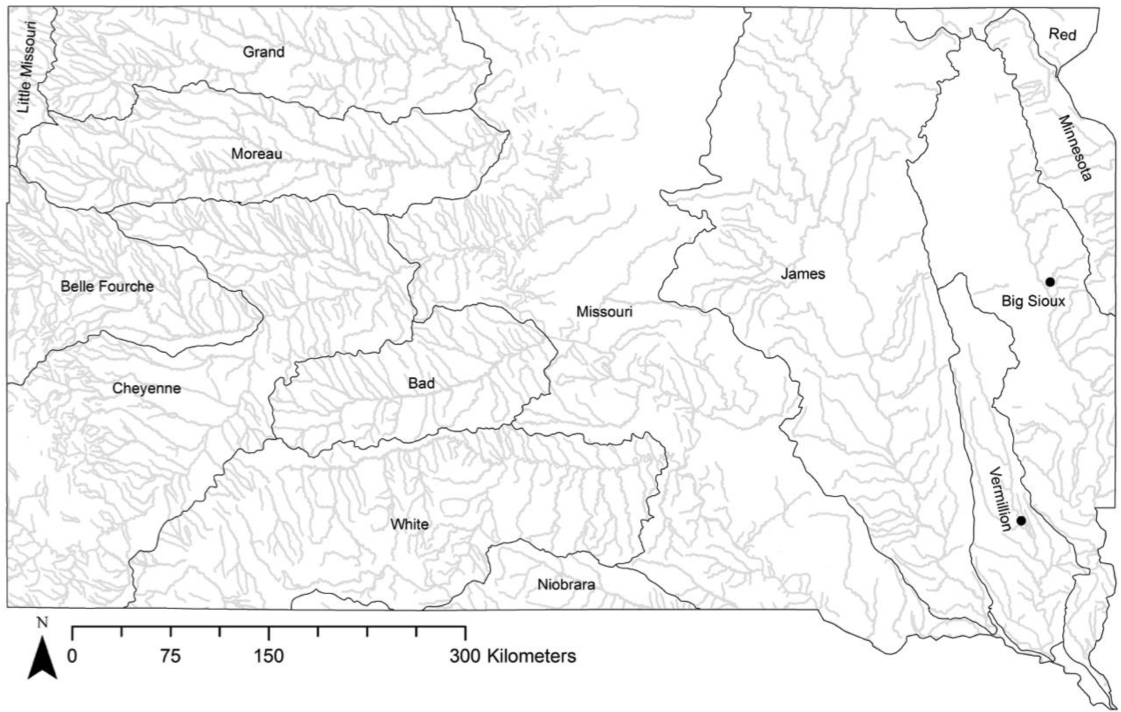


Figure 4: Distribution of *Leptodea fragilis* from the 2014-2015 statewide survey.

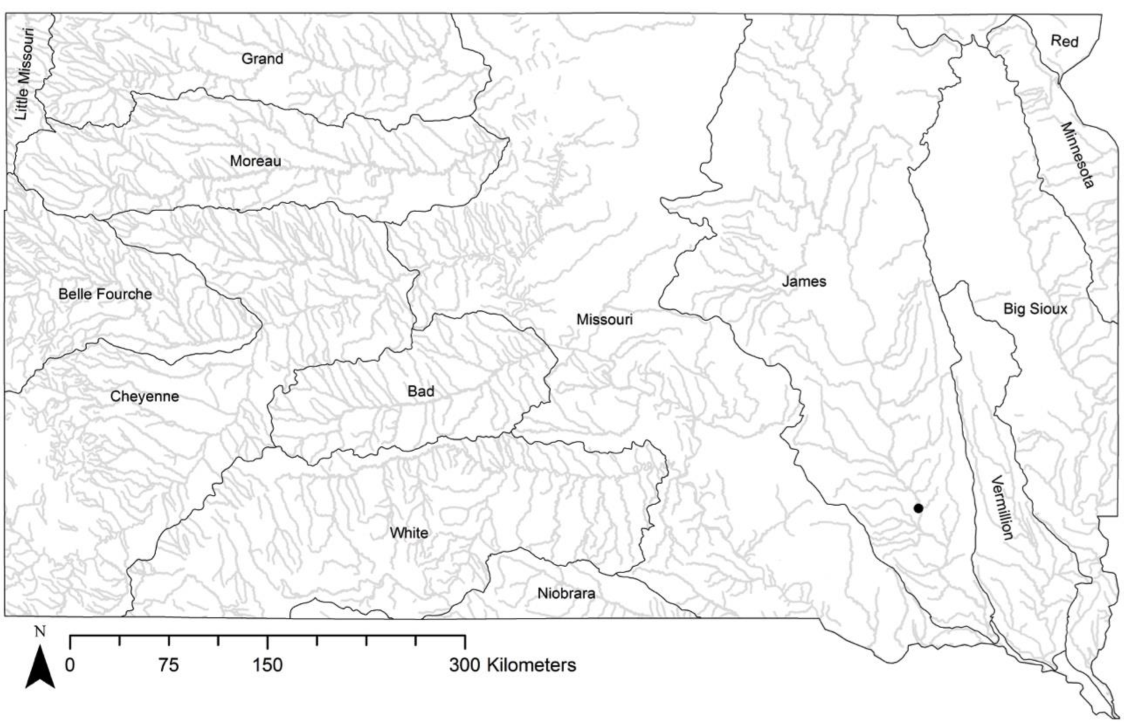


Figure 5: Distribution of *Ligumia recta* from the 2014-2015 statewide survey.

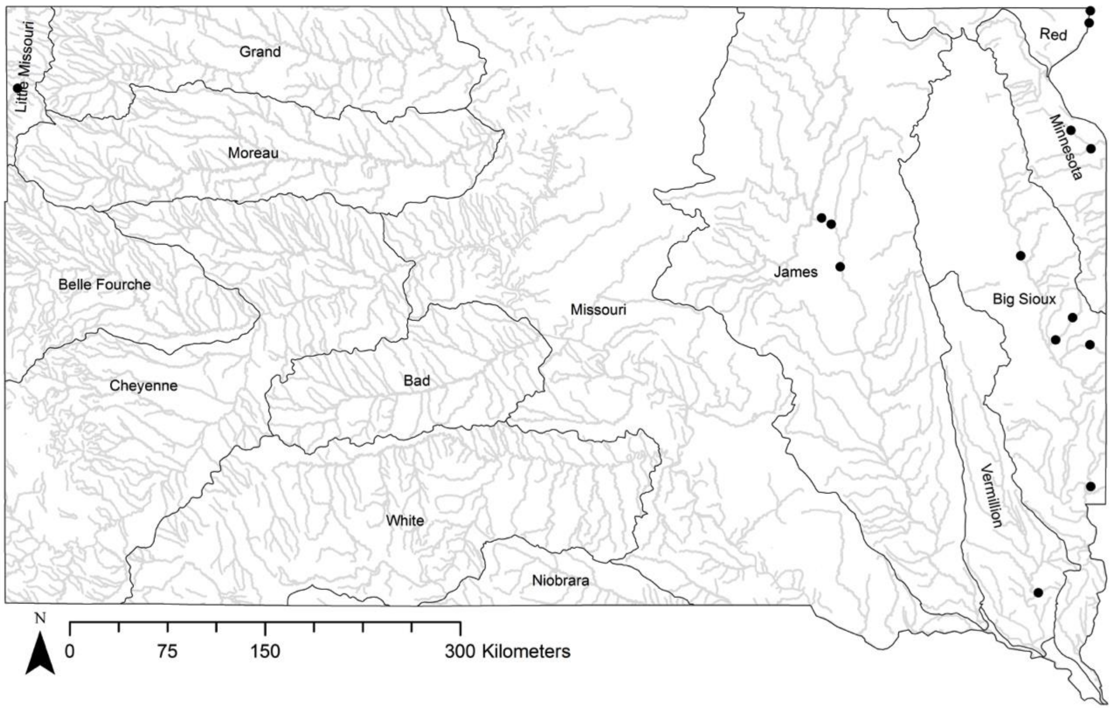


Figure 6: Distribution of *Lampsilis siliquoidea* from the 2014-2015 statewide survey.

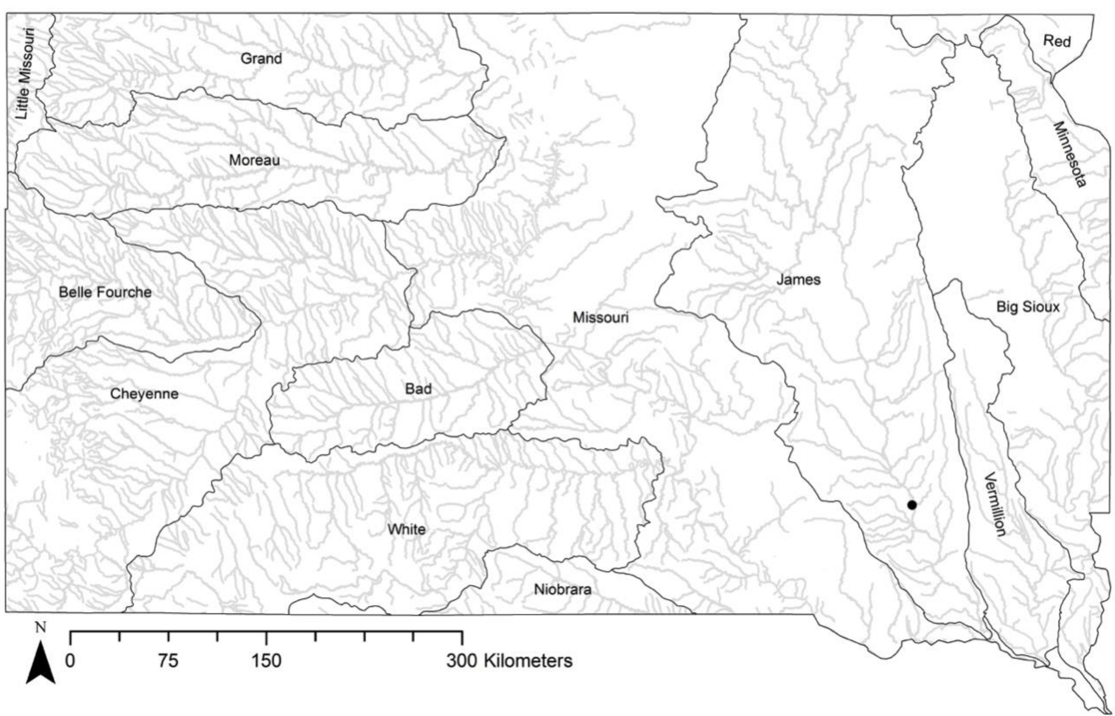


Figure 7: Distribution of *Obliquaria reflexa* from the 2014-2015 statewide survey.

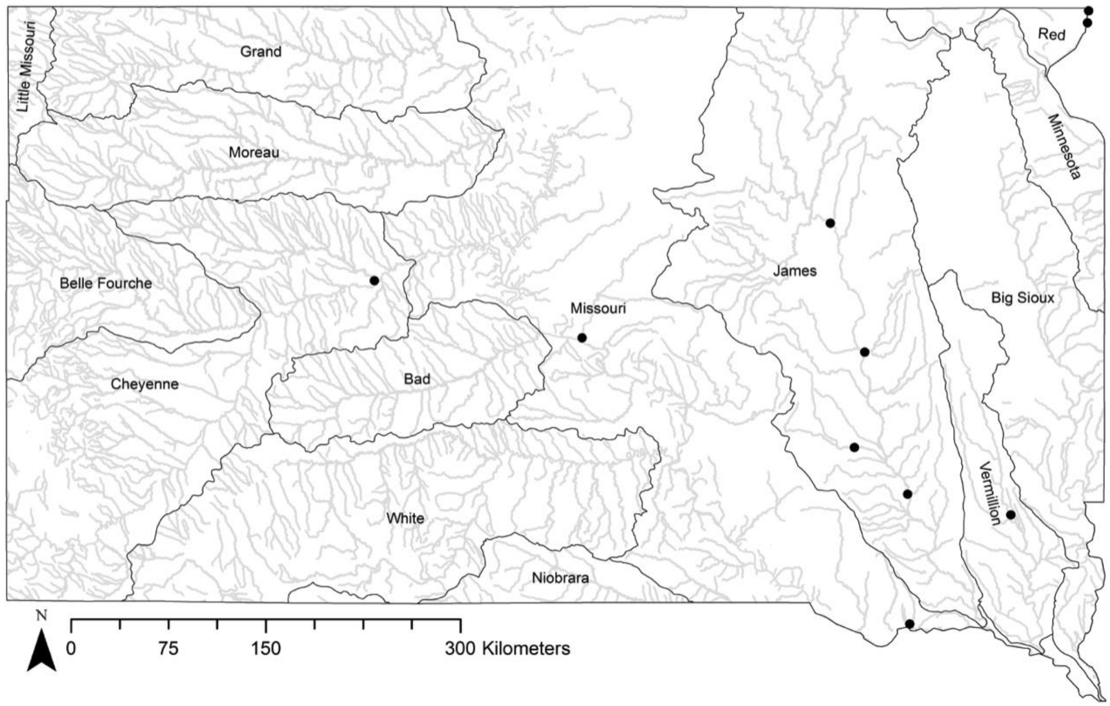


Figure 8: Distribution of *Potamilus alatus* from the 2014-2015 statewide survey.

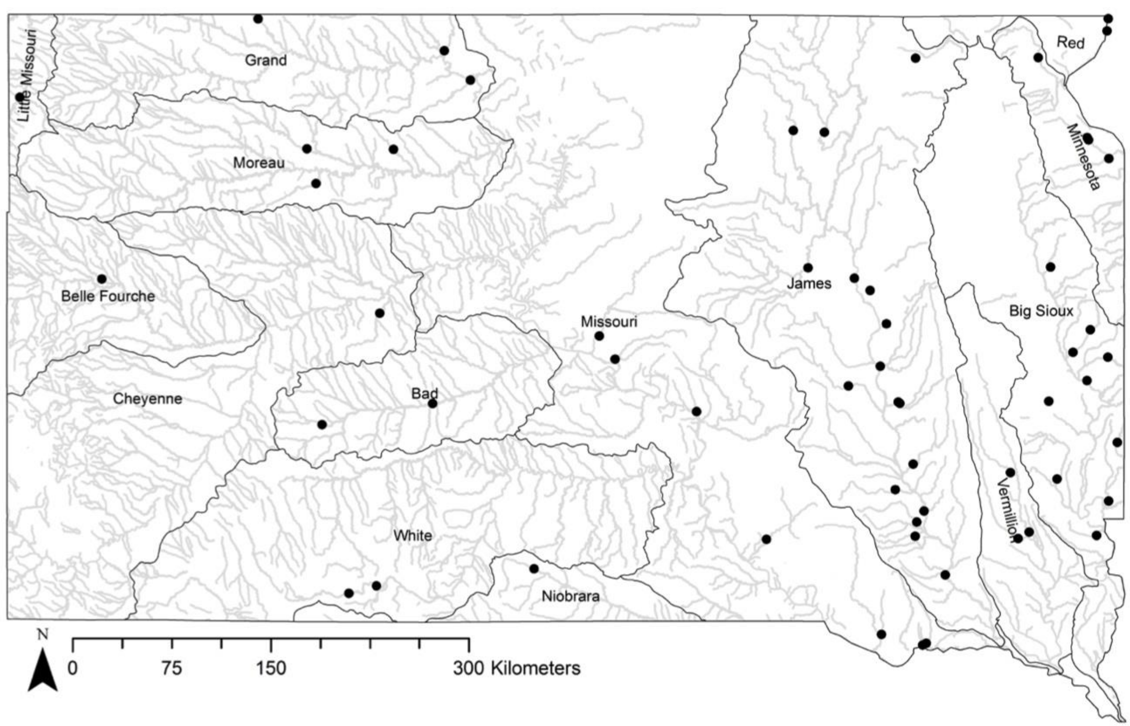


Figure 9: Distribution of *Pyganodon grandis* from the 2014-2015 statewide survey.

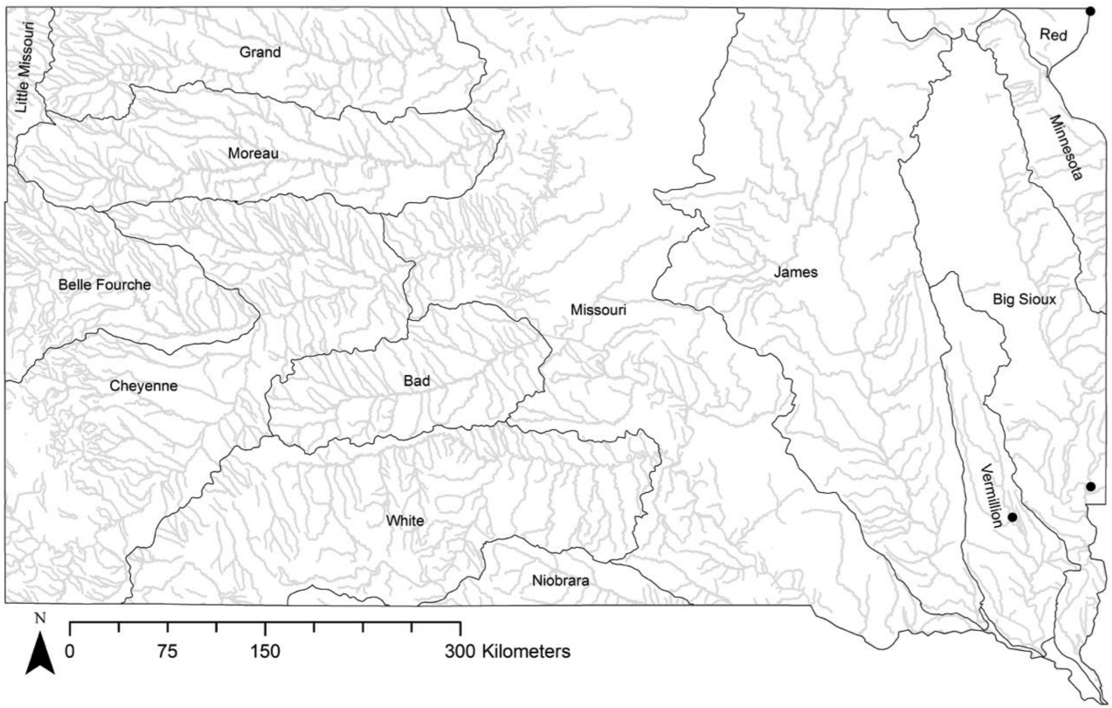


Figure 10: Distribution of *Pleurobema sintoxia* from the 2014-2015 statewide survey.

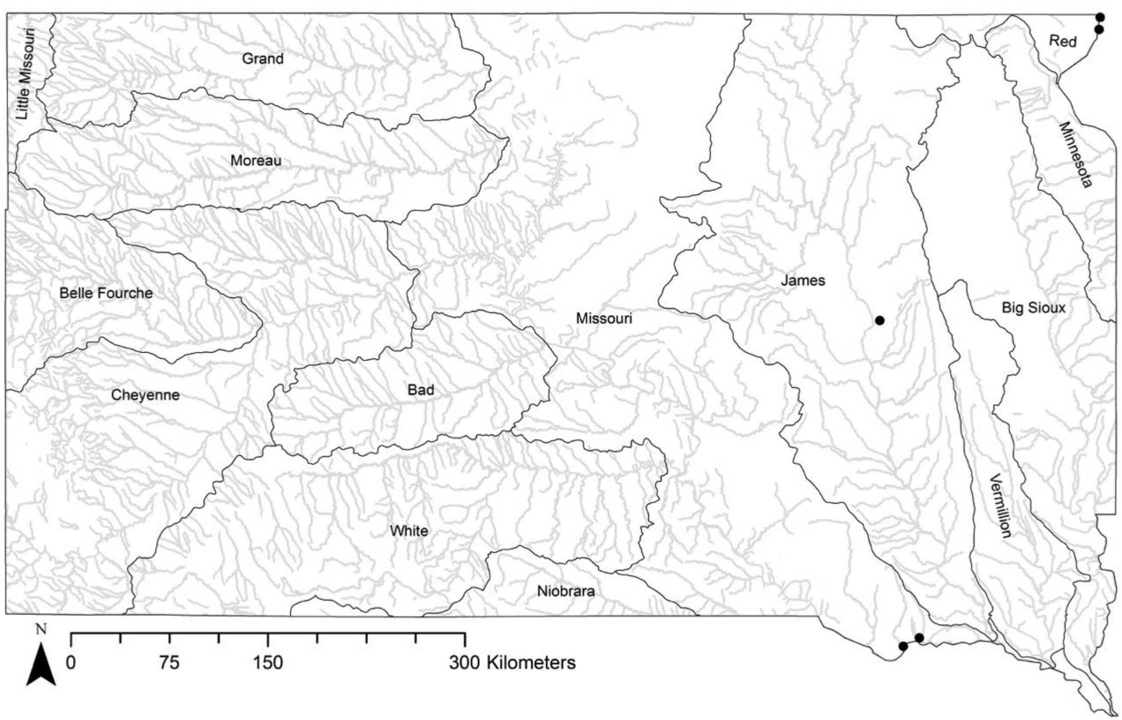


Figure 11: Distribution of *Quadrula quadrula* from the 2014-2015 statewide survey.

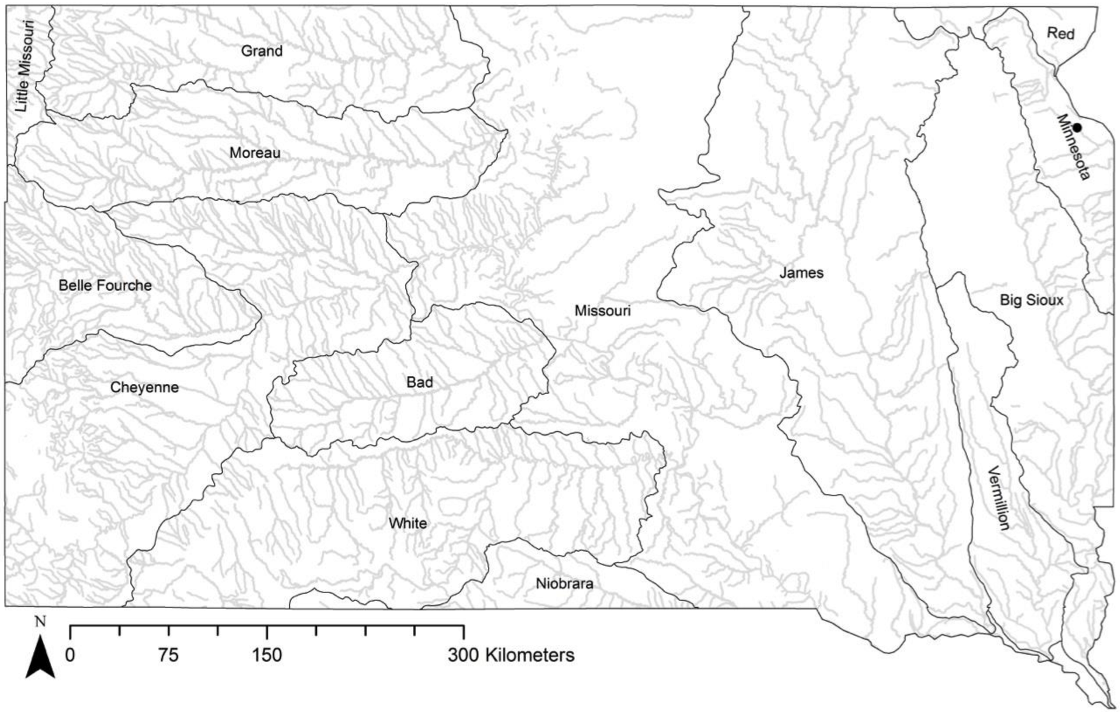


Figure 12: Distribution of *Strophitus undulatus* from the 2014-2015 statewide survey.

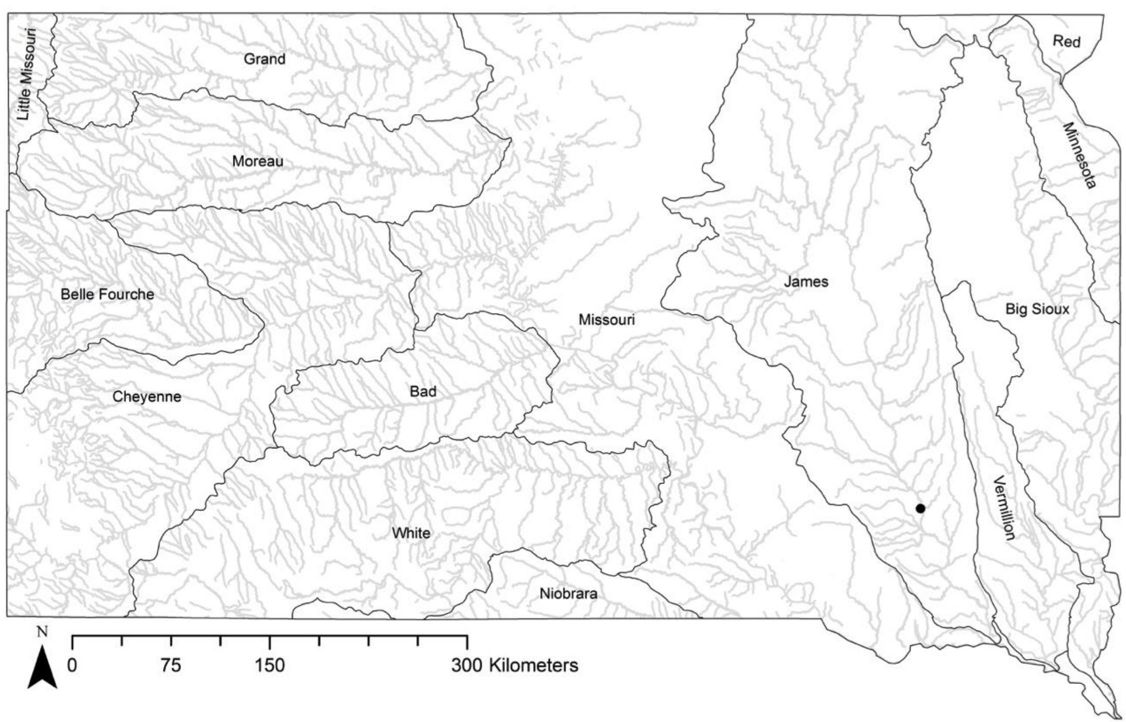


Figure 13: Distribution of *Truncilla truncata* from the 2014-2015 statewide survey.

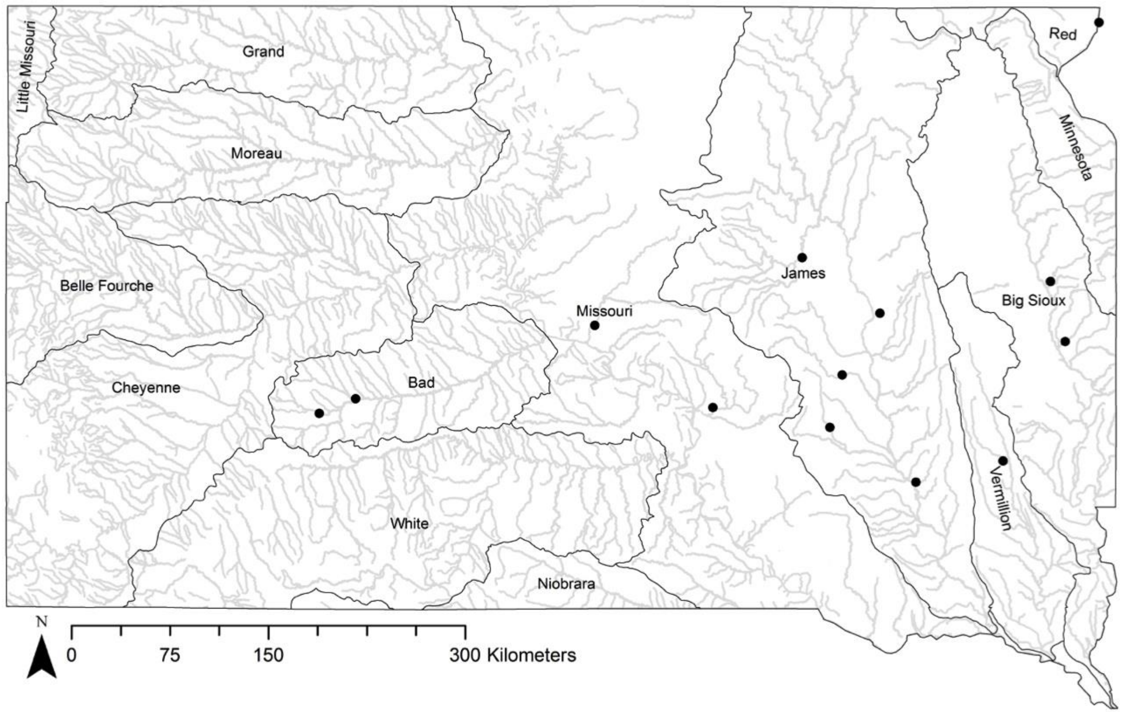


Figure 14: Distribution of *Utterbackia imbecillis* from the 2014-2015 statewide survey.

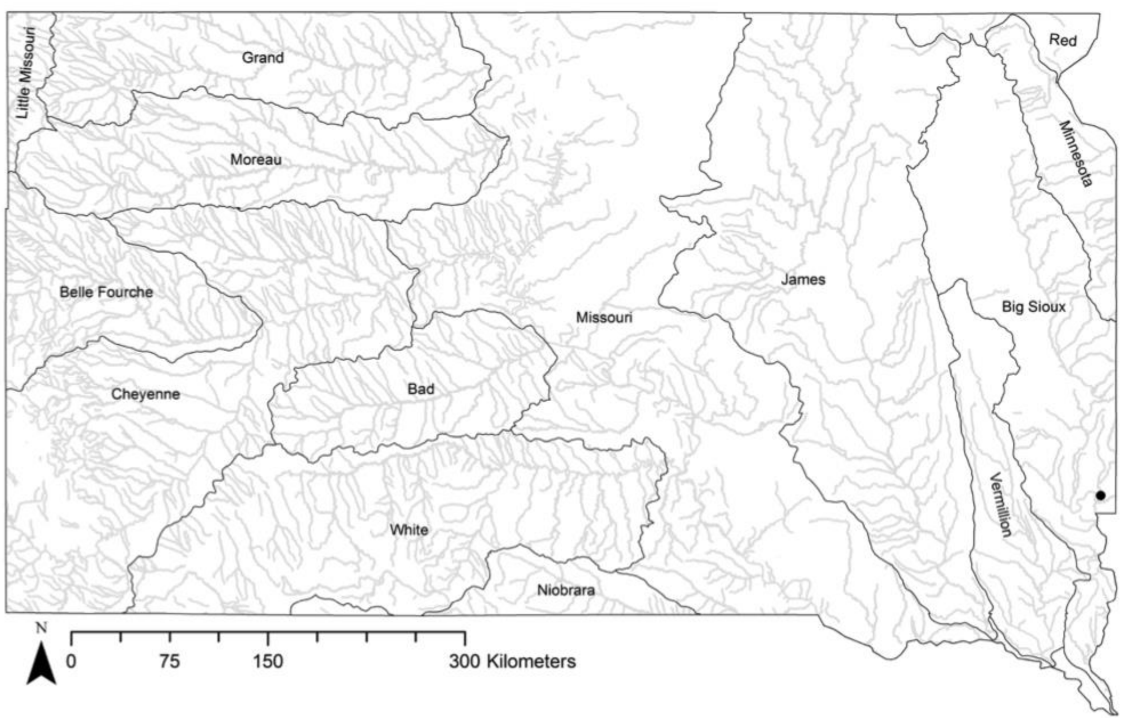


Figure 15: Distribution of *Venustaconcha ellipsiformis* from 2014-2015 statewide survey.

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