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Unionid Mussel Species Distributions and Compositions Observed during a 2014 and 2015 Statewide Survey in South Dakota, USA

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Full Title:	Unionid Mussel Species Distributions and Compositions Observed during a 2014 and 2015 Statewide Survey in South Dakota, USA
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Abstract:	This study surveyed the unionid mussels in South Dakota's wadeable streams in 2014 and 2015. A total of 1,147 mussels were documented and 602 live mussels were observed. Live mussels, remnant shells, or both, were documented in each of the 14 river basins surveyed and at 91 of the 202 survey sites. Live mussels were collected at 22% of the survey sites. Twelve unionid species (Giant Floater, Pyganodon grandis; White Heelsplitter, Lasmigona complanate; Wabash Pigtoe, Fusconaia flava; Fatmucket, Lampsilis siliquoidea; Pink Heelsplitter, Potamilus alatus; Mapleleaf, Quadrula quadrula; Threeridge, Amblema plicata; Black Sandshell, Ligumia recta; Fragile Papershell, Leptodea fragilis; Threehorn Wartyback, Obliquaria reflexa; Creeper, Strophitus undulatus; Deertoe, Truncilla truncate) were identified from live mussels, remnant shells, or both. Fragile Papershell and Threehorn Wartyback were only identified by remnant or dead shells. Mean mussel species richness across all sites was 0.7 ± 0.09 (SE) and ranged from 0-to-7, with the highest mussel diversity and richness occurring in the basins east of the Missouri River. Giant Floater was the most frequently occurring and most abundant species observed. It was 68% of all mussels sampled and collected in all 14 river basins. The remaining species each represented less than 10% of total abundance. Compared to historical surveys, unionid mussel species distribution, richness, and composition has substantially declined.

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SURVEY ARTICLE

Running head: South Dakota mussel distributions

UNIONID MUSSEL DISTRIBUTIONS IN SOUTH DAKOTA, USA, OBSERVED DURING A STATEWIDE SURVEY IN 2014–2015

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ABSTRACT

We conducted a statewide survey of freshwater mussels (family Unionidae) in wadeable streams in South Dakota in 2014 and 2015. We conducted timed searches (2 person-hours/site) at 202 sites distributed among all 14 of the state's major river drainages. We collected a total of 605 live mussels and 543 recently dead shells, representing 13 unionid species. We found mussels in each of the 14 river drainages and at 91 of the 202 sites (45%), and we collected live mussels at 22% of the sites. Species richness varied among drainages from one to ten. Mussel species richness and abundance were higher in drainages east of the Missouri River (mean richness/site = 1.2 ± 0.1, mean abundance/site = 5.5 ± 1.5/hour) compared to western drainages (mean richness/site = 0.2 ± 0.1, mean abundance/site = 0.4 ± 0.2/hour). The Giant Floater was the most widespread and abundant species, occurring in all 14 river drainages and representing 62.1% of all live mussels. Overall, host generalists with an opportunistic life-history strategy dominated mussel assemblages in South Dakota, which may indicate stressful conditions, particularly in western drainages. A compilation of previous records from South Dakota revealed the former presence of 32 species in the state. However, because of differences in sample effort among studies, comparison of our estimates of species richness with estimates from previous surveys at specific sites and in six eastern drainages did not reveal consistent patterns of species loss. Our use of standardized, timed-search methods provides a baseline that can be used to better assess future changes in species richness and distribution and mussel abundance.

KEY WORDS **-** Unionidae, survey, freshwater mussels, South Dakota

INTRODUCTION

Information about freshwater mussel (family Unionidae) distribution in South Dakota, USA, is limited. The first mussel surveys in the early 1900s were geographically restricted and provided little data (Coker and Southall 1915; Over 1942). Subsequent surveys focused mostly on larger streams in eastern South Dakota (Perkins 1975, 2007; Hoke 1983; Frest 1987; Perkins et al. 1995; Skadsen 1998; Perkins and Backlund 2000, 2003; Skadsen and Perkins 2000; Hoke 2003; Wall and Thomson 2004; Ecological Specialists 2005a, b; Shearer et al. 2005). A total of 32 species have been documented east of the Missouri River, including three listed as endangered under the US Endangered Species Act (Higgins Eye, *Lampsilis higginsii*; Scaleshell, *Potamilus leptodon*; Winged Mapleleaf, *Quadrula fragosa*; Table 1). No comprehensive, statewide survey of mussel distributions in South Dakota has been published. Such information is needed to better understand mussel distributions in the state and to serve as a baseline for monitoring future changes in the fauna (Strayer et al. 1994).

We report the results of the first comprehensive, statewide mussel survey of South Dakota. Our study is based on the unpublished survey of Faltys (2016), who sampled 202 sites distributed among all 14 major river drainages in the state. We report the results of this survey and compare our results with past surveys.

METHODS

Study Area

South Dakota lies entirely within the Great Plains region of North America. It contains 14 major river drainages and is bisected by the Missouri River (Fig. 1). All river drainages in the state are within the Missouri River basin except for headwaters of the Minnesota River system (upper Mississippi River basin) and the Red River system (Nelson River basin) in the northeastern part of the state. Substantial environmental and physical differences exist between the eastern and western halves of the state, and strong east-west precipitation and north-south temperature gradients produce distinct regional climates (Johnson et al. 2005). The six river drainages east of the Missouri River (eastern drainages) were glaciated during the Wisconsin glaciation. This area has a continental climate, and most of the original prairie has been converted to row-crop agriculture (Omernik and Griffith 2014; Gewertz and Errington 2015). The eight river drainages west of the Missouri River (western drainages) were not glaciated. This area has a semiarid climate, with rolling plains, buttes and badlands, dominated by short-grass prairie, which is used primarily for livestock production (Sayler 2014). Streams in western South Dakota are prone to intermittency and flash flooding, while eastern South Dakota streams are more hydrologically stable (Chapman et al. 2001).

Mussel Surveys

We surveyed eastern drainages from June 4 to August 14, 2014, and western drainages from May 27 to July 27, 2015. We used ArcGIS (10.1/2012, ESRI, California) to randomly and proportionately select sampling sites on wadeable, perennial mainstem (Missouri River) and tributary streams based on watershed area. We sampled 102 sites in the six eastern river drainages, including the Missouri River, and 100 sites in the eight western drainages (Fig. 1). Sites where landowner permission could not be obtained or where there was a lack of flowing water were replaced with another randomly selected site within the same river drainage.

We conducted 2-person-hour, timed searches at each site following DeLorme (2011). We began timed searches at the nearest access point and moved upstream. We searched the stream bottom for live mussels and empty shells using tactile searches and visual searches with a mask, snorkel, and viewing buckets. We collected all live mussels and recently dead shells and identified them using Cummings and Mayer (1992) and following taxonomy of FMCS (2021). At each site, we retained as vouchers up to two specimens of each species and deposited them in the South Dakota Aquatic Invertebrate Collection, South Dakota State University, Brookings, South Dakota, USA.

For each site, we calculated species richness as the number of species represented by live individuals or recently dead shells. We expressed abundance as catch-per-unit-effort (number live/hour). We categorized host use of each species as a generalist or specialist, and we categorized life-history strategies as opportunistic, periodic, or equilibrium, both based on Haag (2012).

We compared our results to those of previous surveys in three ways. First, we resurveyed seven previously surveyed sites to evaluate changes in the mussel fauna at those sites. All resurveyed sites were in eastern drainages of the Missouri River. We estimated the rate of change in species richness as (current richness – previous richness)/number of years since the previous survey. Second, we compared drainage-wide richness estimates between our survey and 14 previous surveys that provided specific site locations (Table 3). Third, we compared general patterns of species distributions across drainages between our survey and previous surveys (Table 4).

RESULTS

We collected a total of 1,148 mussels (605 live and 543 recently dead shells) across all sites (Table 1; Fig. 1). We detected live or recently dead mussels in all 14 river drainages. Live mussels were observed in all river drainages except the Niobrara and at 45 of 202 sites (22%). We found only recently dead shells at an additional 46 sites (23%), and we found no mussels at 111 sites (55%). We found a total of 13 species, including 12 species represented by living individuals, and one species represented by a single recently dead shell (Pimpleback, *Cyclonaias pustulosa*). Mussel species richness across all sites ranged from zero to seven (mean = 0.7 ± 0.1 SE). We found Zebra Mussels (*Dreissena polymorpha*) at one location in the lower Missouri River (McCook Lake).

Faltys (2016) reported two species not previously documented in South Dakota, the Spike (*Eurynia dilatata*) and the Ellipse (*Venustaconcha ellipsiformis*). After examining photographs and specimens, we determined that both were misidentifications. The specimen identified by Faltys (2016) as a Spike is the Black Sandshell (*Ligumia recta*), and the specimen identified as an Ellipse is the Giant Floater (*Pyganodon grandis*). Additionally, a specimen from the lower Missouri River reported as undetermined by Faltys (2016) is the Paper Pondshell (*Utterbackia imbecillis*).

Mussel species richness and abundance were higher in eastern drainages than in western drainages. All 13 species were found in eastern drainages with total drainage species richness ranging from 5 to 10 (mean richness/site = 1.2 ± 0.1 SE), and abundance of each species ranged from 0 to 81/site (mean CPUE = 2.8/hour ± 0.8 SE, all species combined). In contrast, only four species were found in western drainages, with total drainage species richness ranging from one to two (mean richness/site = 0.2 ± 0.1 SE), and abundance of each live species ranged from 0 to 22/site (mean CPUE = 0.2/hour ± 0.1 SE, all species combined). The highest species richness was found in the James River drainage in eastern South Dakota (10 species) and the lowest species richness was found in the Bad, Moreau, Niobrara, and White River drainages in western South Dakota (1 species in each drainage). The Red River drainage in northeastern South Dakota had the highest abundance (CPUE = 14.5/hour ± 1 SE), and the Niobrara and Moreau River drainages in western South Dakota had the lowest abundance (CPUE = 0, and 0.1/hour ± 0.1 SE, respectively).

The Giant Floater was found in all drainages and was the most abundant species (mean CPUE = 0.931/hour ± 0.3 SE), making up 62.1% of all live mussels (Table 1). The Wabash Pigtoe (*Fusconaia flava*), White Heelsplitter (*Lasmigona complanata*), Pink Heelsplitter (*Potamilus alatus*), Fatmucket (*Lampsilis siliquoidea*), and Mapleleaf (*Quadrula quadrula*) were found in three to eight drainages, and each made up 2.2 to 15.5% of live mussels (Table 1). The remaining six species each were found in one to three drainages and represented less than 1% of live mussels.

We observed fewer species than previous studies at four of seven resurveyed sites (Table 2). The largest decrease in the number of species collected occurred at the Whetstone River site with a potential loss of four species; however, the greatest rates of species loss were observed at the Foster Creek and Redstone Creek sites (0.3 species/year). We observed more species than previous studies at the Bois de Sioux and Vermillion rivers. We observed three new species at the Bios de Sioux River (Threeridge, *Amblema plicata*; Black Sandshell; and Mapleleaf), but we did not find Pink Papershell, *Potamilus ohiensis*, which was reported previously from the site. At the Vermillion River site, we observed four new species (Fragile Papershell, *Potamilus fragilis*, recently dead shells only; Pink Heelsplitter; Threeridge; and Wabash Pigtoe), but we did not find

Creeper (*Strophitus undulatus*), which was reported previously from the site. Species richness was unchanged at the Hidewood Creek site.

Among six eastern drainages, we found lower mean species richness/site than previous studies in three drainages (Big Sioux, James, and Vermillion) and higher richness/site in three drainages (Minnesota, Red, and Missouri River mainstem) (Table 3). The greatest decline in species richness/site was in the James River drainage (0.68 versus 0.23 species/site), and the greatest increase in richness was in the Red River drainage (1.67 versus 3.50 species/site).

General patterns of species distributions across eastern drainages in our study were similar to those of previous studies (Table 4). The four most widely distributed species in our study, Giant Floater (six drainages), White Heelsplitter (six drainages), Fatmucket (five drainages) and Pink Heelsplitter (four drainages), were reported from all six eastern drainages by previous studies. All species that we found in three drainages were reported from four to five drainages by previous studies (Threeridge, Wabash Pigtoe, and Mapleleaf). However, three species that were widespread in previous studies either were not found in our study (Pink Papershell, six drainages previously; Lilliput, *Toxolasma parvum*, five drainages previously) or were found in only one drainage (Creeper, five drainages previously). We did not find four other species that were found in four drainages in previous surveys (Cylindrical Papershell, *Anodontoides ferrusacianus*; Rock-pocketbook, *Arcidens confragosus*; Plain Pocketbook, *Lampsilis cardium*; and Yellow Sandshell, *L. teres*).

The two most widely distributed species in our study, Giant Floater and White Heelsplitter, are host generalists and opportunistic life-history strategists (Table 1). Together, host generalists and opportunistic strategists made up 72.2% and 77.5% of all live mussels encountered, respectively. In contrast, equilibrium and periodic strategists made up only 18.7% and 3.8% of live individuals, respectively.

DISCUSSION

All unionid species we collected were reported from the state by previous surveys (Table 4). We observed 13 species of unionid mussels, far fewer than the 32 species reported in South Dakota from a compilation of previous surveys. This could be interpreted as a greater than 50% decline in species richness in the state. However, because our survey was designed to cover the entire state, including the largely unsurveyed western drainages, sampling effort in each drainage was substantially lower than that expended by combined previous surveys. Furthermore, our probabilistic sampling design was meant to provide an unbiased depiction of mussel distribution and abundance at a large scale. In contrast, most previous surveys focused on sites or habitats that were considered likely to support mussels. For these reasons, we are unable to conclude whether species richness has declined overall in the state since previous surveys. Our comparisons of species richness at previously surveyed sites and in six eastern drainages indicated possible declines in richness in only about half of the cases, and no change or possible increases in richness in the other cases. These differences in species richness estimates among studies may be due to differences in sampling effort, sampling methods, or other factors (Metcalfe-Smith et al. 1998).

Unionid surveys conducted in states bordering South Dakota have noted declines in species richness (Badra and Goforth 2003; MNDNR 2004; Poole and Downing 2004; Fisher 2006; Obermeyer et al. 2006; Roberts et al. 2008; DeLorme 2011; Grabarkiewicz and Gottgens 2011; Hoke 2011; Stodola et al. 2013). The causes of these declines are unknown, but they have been attributed to degraded water quality and aquatic habitats and hydrological changes resulting from conversion of grassland to row-crop agriculture (Allan 2004; Downing et al. 2010). Widespread conversion of grassland to row-crop agriculture and accompanying negative effects on streams also has occurred in South Dakota (Johnston 2013; Wright and Wimberly 2013), and it is likely that these factors have negatively affected the state's mussel fauna.

Other factors may pose threats to the mussel fauna of South Dakota. The four dams on the Missouri River and thousands of small impoundments on tributaries alter mussel habitat and host-fish distribution in streams (Watters 2000; Haag 2012). In addition, 22 nonindigenous fish species occur in South Dakota, and they may displace native fish species (Saunders et al. 2002; Hoagstrom et al. 2007). Decreases or changes in host-fish communities could negatively impact mussel recruitment (Douda et al. 2013; Galbraith et al. 2018). However, eight of the mussel species we collected are host specialists, suggesting that changes in the fish fauna would produce species-specific effects on the mussel fauna rather than fauna-wide effects (Haag 2019). Two invasive bivalve species occur in South Dakota, the Asian Clam (*Corbicula fluminea*) and the Zebra Mussel, both of which can pose serious threats to native species (Schneider et al. 1998; Shearer et al. 2005; Huber and Geist 2019; Vanderbush et al. 2021). Finally, changes in temperature, streamflow, runoff, and salinity due to climate change can negatively impact aquatic ecosystems and species, potentially including mussels **(**Hastie et al. 2003; Ganser et al. 2013; Inoue and Berg 2017).

Overall, the mussel fauna of South Dakota is dominated by species with generalist host-use and an opportunistic life-history strategy. Species with those traits generally are considered tolerant of stressful conditions, and their dominance in mussel assemblages can indicate habitat degradation (Morris and Corkum 1996; Metcalfe-Smith 1998; Hornbach et al. 2019). In addition to their lower species richness, drainages west of the Missouri River were composed almost entirely of opportunists or host generalists. This finding probably indicates that mussel populations in that region are limited naturally by arid conditions and hydrological instability, in addition to human factors. In contrast, host specialists and species with periodic or equilibrium life-history strategies were found predominantly in eastern drainages. This finding could mean that there are fewer environmental stressors and disturbances within these drainages, which allows persistence of life-history strategies that require more stable conditions (Haag 2012).

Timed-search visual and tactile survey methods as used in our study are appropriate for surveys designed to assess patterns of species richness and distribution at large scales. In contrast, quadrat-based methods are more labor intensive and may underestimate species richness, particularly when mussel abundance is low (Hornbach and Deneka 1996), as is often the case in South Dakota. Visual and tactile methods can be biased by habitat or sampling conditions, but standardized application of these methods can provide cost-effective, useful comparisons of mussel abundance and species richness over time (Metcalf-Smith et al. 2000; Wisniewski 2013). Our ability to assess long-term changes in species richness was limited by the large differences in sampling effort between our study and previous studies. Using standardized, timed-search methods can allow more informative assessments of changes in species distribution and richness over time that avoid the difficulties of comparing qualitative, historical records with contemporary surveys (e.g., Angelo et al. 2009). In addition, our estimates of CPUE provide a baseline that can allow assessment of changes in mussel abundance over time.

Due to their relatively sedentary lifestyle, mussel presence and population health are strongly tied to the occurrence of suitable host fish and habitat. Habitat suitability modeling can be used to refine monitoring efforts and conservation planning by identifying priority areas for sampling or conservation efforts (Daniel et al. 2018). Additionally, environmental DNA (eDNA) can be used as a tool to quickly screen wide geographical areas, which is particularly important when the full extent of target species ranges is unknown (Gasparini et al. 2020; Lor et al. 2020; Rodgers et al. 2022). Incorporating habitat suitability modeling and eDNA sampling can augment and guide future monitoring surveys for freshwater mussels in South Dakota.

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FIGURE LEGENDS

Figure 1. Sites surveyed for freshwater mussels in 14 river drainages in South Dakota in 2014–2015. Solid circles indicate sites at which live mussels were found. Open circles represent sites at which only recently dead shells were found, and "x" represents sites at which no evidence of mussel presence was found. Open square indicates historic resurvey site locations (N = 7). The inset map shows the location of South Dakota in the continental USA.

Table 1. Mussel species collected in all 14 river drainages of South Dakota in 2014 and 2015. Numbers in parentheses after drainage name indicate the number of sites sampled. "L" indicates species found live, "X" indicates species found only as recently dead shells, and "–" indicates that the species was not found. CPUE = catch-per-unit-effort (number of live mussels/hour). Relative abundance is reported for live mussels. Fish-host use was determined following Haag (2012) where "G" indicates host generalist and "S" indicates host specialist. Life-history strategies were determined following Haag (2012) where "O" indicates opportunistic, "P" indicates periodic, and "E" indicates equilibrium.

			Eastern drainages						Western drainages											
Species	Fish host	Life history Strategy	Big Sioux (20)	James (39)	Minnesota (6)	Missouri (26)	Red (2)	Vermillion (9)	Bad (9)	Belle Fourche (9)	Cheyenne (27)	Grand (13)	Little Missouri (2)	Moreau (14)	Niobrara (3)	White (23)	Number live & dead	Number live	CPUE	Relative abundance %
Pyganodon grandis	G	O	L	L	L	L	L	L	L	L	X	L	L	L	X	L	784	376	0.931	62.1
Fusconaia flava	S	E	–	X	L	–	–	X	–	–	–	–	–	–	–	–	103	94	0.233	15.5
Lasmigona complanata	G	O	X	L	L	L	L	L	–	L	–	L	–	–	–	–	141	54	0.134	8.9
Potamilus alatus	S	O	–	L	–	L	L	X	–	–	L	–	–	–	–	–	51	35	0.087	5.8
Lampsilis siliquoidea	S	P	L	L	L	–	L	X	–	–	–	–	L	–	–	–	56	20	0.049	3.3
Quadrula quadrula	S	E	–	L	–	L	L	–	–	–	–	–	–	–	–	–	15	13	0.032	2.2
Amblema plicata	G	E	X	–	–	–	L	X	–	–	–	–	–	–	–	–	8	6	0.015	1.0
Ligumia recta	S	P	–	X	–	–	L		–	–	–	–	–	–	–	–	4	2	0.005	0.3
Potamilus fragilis	S	O	X	L	–	–	–	X	–	–	–	–	–	–	–	–	4	2	0.005	0.3
Cyclonaias pustulosa	S	E	–	X	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0.000	0.0
Strophitus undulatus	G	P	–	–	L	–	–	–	–	–	–	–	–	–	–	–	1	1	0.002	0.2
Truncilla truncata	S	O	–	L	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0.002	0.2
Utterbackia imbecillis	G	O	–	–	–	L	–	–	–	–	–	–	–	–	–	–	1	1	0.002	0.2
Drainage richness			5	10	5	5	7	7	1	2	2	2	2	1	1	1	Total	Total		
Drainage CPUE			0.4	3.1	12.9	1.2	14.5	1.4	0.3	1.2	0.02	0.1	0.8	0.1	0	0.3	1148	605		

Table 2. Comparisons of mussel species richness between this study (current, 2014–2015) and previous surveys at seven sites in eastern South Dakota. CPUE = catch-per-unit-effort (number of live mussels/hour) in this study. Superscripted numbers represent sources for previous surveys.

Stream	Drainage	Site richness		
		Previous	Current (CPUE)	Change/year
Vermillion River[1]	Vermillion	3	6 (1)	0.08
Big Sioux River[4]	Big Sioux	1	0 (0)	-0.07
Bois de Sioux River[2]	Red	5	7 (15)	0.11
Foster Creek[5]	James	4	1 (0)	-0.30
Hidewood Creek[3]	Big Sioux	3	3 (0.5)	0.00
Redstone Creek[5]	James	4	1 (0.5)	-0.30
Whetstone River[2]	Minnesota	8	4 (11.5)	-0.21

[1]Perkins (1975); [2]Perkins et al. (1995); [3]Skadsen (1998); [4]Skadsen and Perkins (2000); [5]Wall and Thomson (2004).

Table 3. Comparisons of mussel species richness between this study (current, 2014–2015) and previous surveys in six river drainages in eastern South Dakota. Superscripted numbers represent sources for previous surveys.

Drainage	Time period	Number of sites	Mean richness/site (Total richness)
Big Sioux[3,5]	Previous	75	0.35 (26)
	Current	20	0.25 (5)
James[7,8]	Previous	34	0.68 (23)
	Current	39	0.23 (9)
Minnesota[2]	Previous	56	0.21 (12)
	Current	6	0.83 (5)
Missouri[4,6,9,10,11,12,13,14]	Previous	233	0.09 (20)
	Current	26	0.19 (5)
Red[2]	Previous	3	1.67 (5)
	Current	2	3.50 (7)
Vermillion[1]	Previous	13	1.00 (13)
	Current	9	0.78 (7)

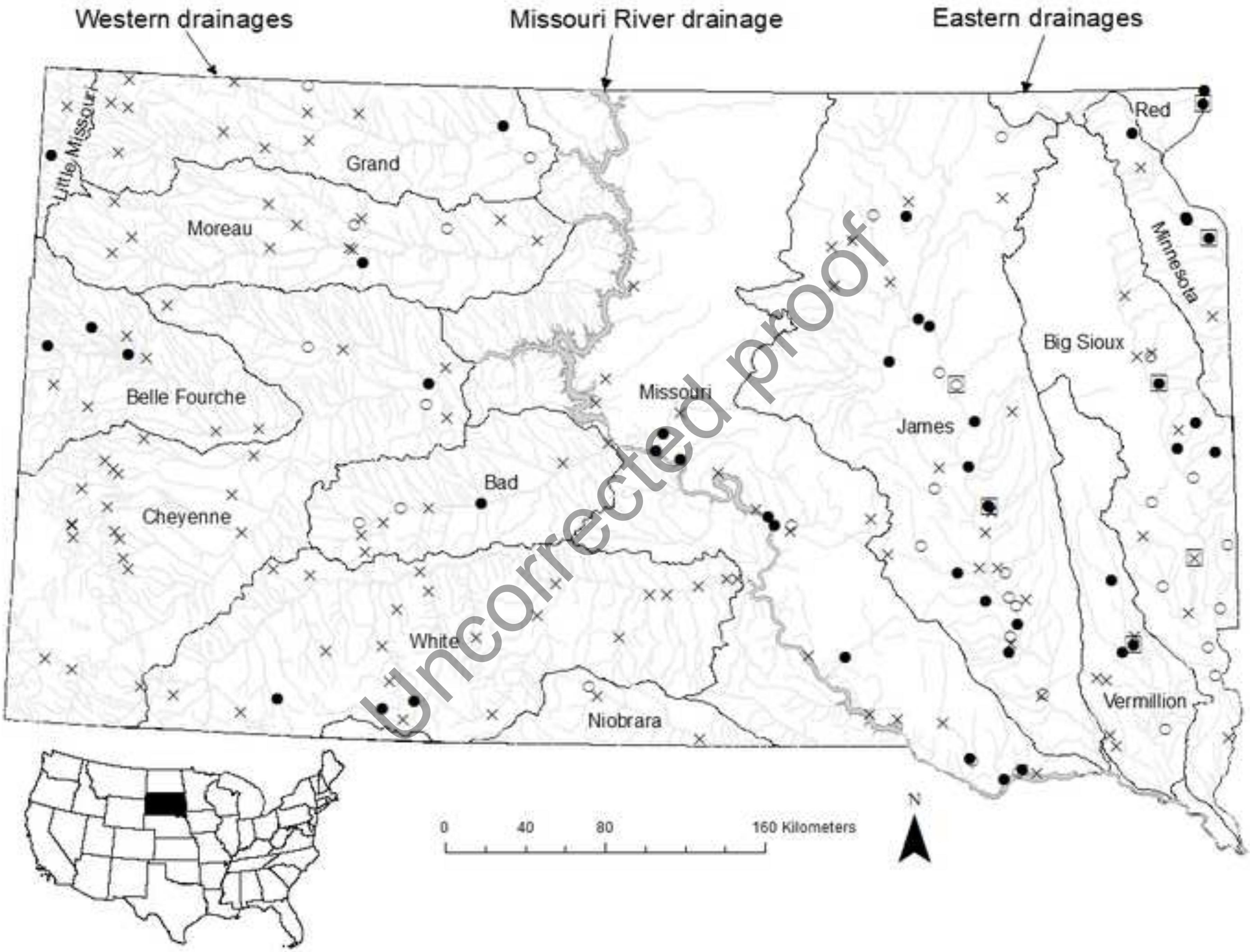
[1]Perkins (1975); [2]Perkins et al. (1995); [3]Skadsen (1998) [4]Perkins and Backlund (2000); [5]Skadsen and Perkins (2000); [6]Hoke (2003); [7]Perkins and Backlund (2003); [8]Wall and Thomson (2004); [9]Ecological Specialists, Inc. (2005a); [10]Ecological Specialists, Inc. (2005b); [11]Shearer et al. (2005); [12]Perkins (2007); [13]Ecological Specialists, Inc. (2007); [14]Ecological Specialists, Inc. (2012).

Table 4. Comparison of mussel species occurrence and richness between this study (C = current, 2014-2015) and previous surveys (P = 14 previous surveys, 1975–2012) in six river drainages in eastern South Dakota. Fish-host strategies are G, generalist and S, specialist (Haag 2012). Life-history strategies are O, opportunistic, P, periodic, and E, equilibrium (Haag 2012). "L" indicates species found live, "FD" indicates species found as recently dead shells, "WD" indicates species found as weathered dead shells, "X" indicates species presence but unreported condition, and "–" indicates that the species was not found. Superscripted numbers represent sources for previous surveys.

			Big Sioux [1,2,5,7]		James [1,2,9,10]		Minnesota[4]		Missouri [6,8,11,12,13,14,15,16]		Red[4]		Vermillion [1,2,4]	
Species	Fish Host	Life History Strategy	P	C	P	C	P	C	P	C	P	C	P	C
Alasmidonta marginata	G	P	X	–	–	–	–	–	–	–	–	–	–	–
Amblema plicata	G	E	L	FD	L	–	–	–	L	–	–	L	L	FD
Anodontoides ferussacianus	G	O	X	–	X	–	L	–	–	–	–	–	L	–
Arcidens confragosus	G	O	WD	–	X	–	–	–	WD	–	–	–	X	–
Cyclonaias pustulosa	S	E	X	–	L	–	–	–	L	–	–	–	–	–
Cyclonaias tuberculata	S	E	X	–	–	–	–	–	–	–	–	–	–	–
Fusconaia flava	S	E	X	–	X	FD	L	L	–	–	–	–	X	FD
Lampsilis cardium	S	P	X	–	X	–	X	–	–	–	–	–	X	–
Lampsilis higginsii	S	P	–	–	–	–	–	–	X	–	–	–	–	–
Lampsilis siliquoidea	S	P	L	L	X	L	L	L	L	–	X	L	X	FD
Lampsilis teres	S	O	FD	–	X	–	–	–	L	–	–	–	X	–
Lasmigona complanata	G	O	L	L	L	L	L	L	L	L	X	L	L	L
Lasmigona compressa	S	O	X	–	–	–	X	–	–	–	–	–	–	–
Ligumia recta	S	P	X	–	X	FD	–	–		–	–	L	X	–
Obliquaria reflexa	S	P	WD	–	FD	FD	–	–	–	–	–	–	–	–
Obovaria olivaria	S	P	FD	–	FD	–	–	–	–	–	–	–	–	–
Pleurobema sintoxia	S	E	X	–	X	–	–	–	–	–	–	–	X	–
Potamilus alatus	S	O	X	–	X	L	L	–	L	L	L	L	L	FD
Potamilus fragilis	S	O	L	FD	L	–	X	–	L	–	–	–	L	FD

Potamilus leptodon	S	O	–	–	–	–	–	–	FD	–	–	–	–	–
Potamilus ohiensis	S	O	L	–	L	–	X	–	L	–	X	–	X	–
Pyganodon grandis	G	O	L	L	L	L	L	L	L	L	L	L	L	L
Quadrula fragosa	S	E	WD	–	WD	–	–	–	–	–	–	–	–	–
Quadrula quadrula	S	E	L	–	L	L	–	–	L	L	–	L	L	–
Sagittunio subrostratus	S	O	FD	–	FD	–	–	–	X	–	–	–	–	–
Strophitus undulatus	G	P	X	–	FD	–	L	L	WD	–	–	–	L	–
Toxolasma parvum	S	O	L	–	X	–	X	–	L	–	–	–	X	–
Tritogonia verrucosa	S	E	L	–	X	–	–	–	–	–	–	–	–	–
Truncilla donaciformis	S	O	WD	–	FD	–	–	–	WD	–	–	–	–	–
Truncilla truncata	S	O	WD	–	L	L	–	–	L	–	–	–	L	–
Utterbackia imbecillis	G	O	–	–	–	–	–	–	L	–	–	–	–	–
Utterbackiana suborbiculata	G	O	–	–	–	–	–	–	L	–	–	–	–	–
Total Richness			28	5	25	9	12	5	20	4	5	7	18	7

[1]Coker and Southall (1915); [2]Over (1942); [3]Perkins (1975); [4]Perkins et al. (1995); [5]Skadsen (1998) [6]Perkins and Backlund (2000); [7]Skadsen and Perkins (2000); [8]Hoke (2003); [9]Perkins and Backlund (2003); [10]Wall and Thomson (2004); [11]Ecological Specialists, Inc. (2005a); [12]Ecological Specialists, Inc. (2005b); [13]Shearer et al. (2005); [14]Perkins (2007); [15]Ecological Specialists, Inc. (2007); [16]Ecological Specialists, Inc. (2012).


Western drainages
Missouri River drainage
Eastern drainages
Little Missouri
Grand
Moreau
Belle Fourche
Cheyenne
Bad
White
Niobrara
Missouri
James
Red
Minnesota
Big Sioux
Vermillion
0
40
80
160 Kilometers
N