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The Freshwater Mussels (*Mollusca: Bivalvia: Unionidae*) Of the Channelized Missouri River

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The lower Missouri River has historically been viewed as a faunal barrier for unionids due to high sediment load. However this survey of the lower (channelized) Missouri River documented the presence of 14 unionid species and the exotic *Corbicula fluminea* (Muller, 1774). Unionids are present in stable substrates sheltered from the effects of the river's strong currents. Analysis of early literature on the Missouri River suggests reports of an absence of unionids were not based upon thorough fieldwork, and the most commonly cited rationale for their reported absence, the high sediment load in the river, is not convincing. Pre-1938 unionid vouchers from the middle Missouri River in South Dakota contradict reports of their absence in that sector, and it seems likely that a lack of thorough early field work in the lower Missouri River may explain their perceived historic absence in that sector as well. At present, substrate instability and low winter water levels preclude unionid habitation over much of the lower Missouri River, and erosion silt probably limits unionid diversity in some habitats. These same factors probably exerted similar influences upon unionids in the historic lower Missouri River, with substrate instability and low winter flows precluding establishment of any unionid populations in most Missouri River substrates, and the high silt content of the water restricting unionid diversity to a few silt tolerant species in most viable habitats.

INDEX DESCRIPTORS: freshwater mussels, unionids, Missouri River, *Unionidea*, *Bivalvia*, *Mollusca*.

INTRODUCTION

Originating at the confluence of the Madison, Gallatin, and Jefferson rivers in southwestern Montana, and flowing some 3,971 kilometers to its juncture with the Mississippi River just north of St. Louis, the Missouri is the longest river in the United States (Fig. 1). In this paper, the Missouri River is divided into three sectors: upper, middle, and lower. The upper Missouri includes reaches from the headwaters to the Milk River confluence in east central Montana. The middle Missouri encompasses reaches south and east of the upper sector to Ponca State Park in northeastern Nebraska. The lower Missouri River, the subject of this study, includes the remaining reaches south and eastward to the confluence with the Mississippi.

Today the Missouri River is one of the most highly regulated rivers in the United States. Six major dams were constructed on the river between 1934 and 1963 in east-central Montana, North Dakota, South Dakota, and northern Nebraska creating reservoirs that inundate its floodplain in much of Montana, almost all of the Dakotas, and along a portion of the Nebraska-South Dakota border. Between these reservoirs, the Missouri is free flowing in only four segments encompassing a total of 547 of an original 1,548 river kilometers. Below Lewis and Clark Lake, the river flows free for 91 kilometers to Ponca State Park in northeastern Nebraska. The 1,262 kilometers below the park have been channelized, and river banks in this sector are generally lined with rock fill and or studded with rows of wing dams. Almost all of the islands, chutes (side-channels), and backwaters formerly abundant in this sector have been eliminated.

The Missouri River drains an immense basin of approximately 1,370,000 km^2 that encompasses portions of Missouri, Kansas, Iowa, Colorado, Wyoming, Minnesota, South Dakota, North Dakota, Montana, and Canada, as well as the entire state of Nebraska. Despite its size and importance from a geographic perspective, the freshwater mussels of the Missouri River were historically almost unstudied. Populations of *Margaritifera margaritifera* (Linnaeus, 1758) and *Lampsilis siliquoidea* (Barnes, 1823) have long been known from the upper Missouri River in western Montana (Bland and Cooper, 1861; Cooper, 1869; Henderson, 1924); however, there are almost no early reports of mussels in eastward locales. In fact, there was a general belief that mussels could not survive in the middle and lower sectors of the Missouri River (Hayden, 1862; Coker and Southall, 1915; Utterback, 1915–1916, 1917; Over, 1915, 1942), and Bartsch (1916) described the Missouri as a faunal barrier for unionids due to the high silt content of its waters and speculated mussels were smothered by the sediment load.

Since 1983, unionids have been reported from reaches formerly believed to be uninhabitable, primarily along the South Dakota – Nebraska border (Hoke, 1983, 2005a; Clarke, 1996; Perkins and Backlund, 2000; Shearer et al., 2005), though a few sites have been sampled in Montana (Gangloff and Gustafson, 2000) and a greater number from Missouri River impoundments in South Dakota (Ecological Specialists, Inc., 1998; Backlund, 2000; Hoke, 2003). With the exception of seven sites reported from the channelized sector by Hoke (1983), the unionid fauna of the lower Missouri River has not been studied. It was therefore decided to expand this initial effort to encompass the entire lower Missouri. The primary goals were: (1) to obtain base-line data on extant freshwater mussel populations; (2) to understand the habitats currently utilized; and (3) to provide insight into the river's historic fauna and habitats.

METHODS

Collections were made at sites along the Missouri River from its mouth above St. Louis, Missouri to Ponca State Park

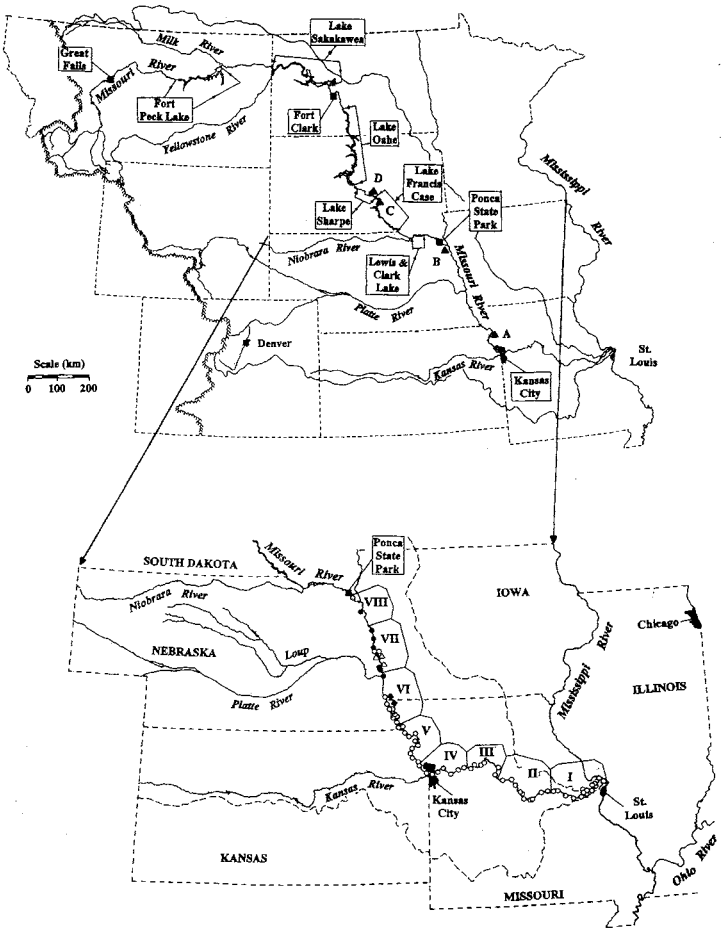

Fig. 1(upper). The Missouri River Basin subsequent to the closing of the six major dams along the upper and middle Missouri River. Filled triangles and associated capital letters denote pre- 1938 collection sites documented by extant unionid vouchers from the Missouri River and its floodplain as follows: A = Utterback (1915–1916); B = Crystal Lake, Nebraska (University of Michigan Museum of Zoology, specimen numbers 7663 and 7718); C = Chamberlain, South Dakota (University of Colorado Museum of Natural History, specimen numbers 15116 and 15117); and D = Crow Creek Agency, South Dakota (United States National Museum, specimen number 676897). Fig. 1(lower). Freshwater mussel collection regions and sites in and along now channelized reaches of the lower Missouri River. Roman numerals indicate collection regions. Collection locales are indicated as follows: triangles denote museum collection locales; filled circles are sites previously reported in Hoke (1983); open circles indicate collection sites sampled in this study; and the filled diamonds in region VI indicate the location of floodplain ditches reported by Hoke (2005b).

(Nebraska), the upper end of the channelized river. The focus of the survey was upon the fauna of the Missouri River main stem, however, a number of sites were also sampled in floodplain habitats. Most survey activity occurred between 1988 and 1990, though limited work was conducted in 1982, 1983, and 2000. The sites selected for sampling were strongly influenced by the ability to obtain access to the river, and many were near highway bridges and other public access points. Pierce (1983) was especially useful in locating access points along the lower 886 kilometers of the river.

Sites examined extended as much as 2.0 km up or down river from the entry point. Accessible areas were searched until shells were encountered, and productive habitats were then sampled until diversity plateaued, or the accessible portion had been covered. Collecting time per site varied from one-half to three hours, and averaged one hour. Mussels were collected by hand, or with a garden rake, usually in the late fall and winter, when flows from upstream reservoirs are minimized, and water levels are comparatively low. Unless otherwise noted, locales reported in this study were sampled by the author.

Sampling was qualitative, but the most common species were often recorded. Field notes were prepared at all collection sites and emphasized observations of environmental factors associated with the presence or absence of freshwater mussels. In addition, a photographic record was produced at most sites. An attempt was made to sample all of the habitats present in and along the Missouri River. The habitats identified for sampling were sandbars, pools below wing dams, side channels, detached lakes, sloughs, backwaters, revetments, and accessible portions of the main channel. Species specific habitat preferences were deduced from the presence of live mussels or shells embedded in normal position in exposed substrates.

Specimens of every species recovered at each site were retained to document the study. All specimens were classified based upon the relative condition (weathering) of the shells; identified by the author; and verified as needed by Drs. David H. Stansbery and G.

Table 1. Freshwater mussels (*Unionidae*) and exotic bivalves collected from the channelized Missouri River and adjacent floodplain habitats by collection region, giving the number of productive sites for each species indicated (species occurrences). Results for regions VI thru VIII include species occurences from Hoke (1983) as noted.

SPECIES	REGION								Total
	I	II	III	IV	V	VI[a]	VII[b]	VIII[c]	
Anodonta suborbiculata (Say, 1831)	7	3	2	-	3	1	3	2	21
Lampsilis teres (Rafinesque, 1820)	1	3	-	1	2	-	1	-	8
Lasmigona c. complanata (Barnes, 1823)	3	-	1	-	1	-	1	1	7
Leptodea fragilis (Rafinesque, 1820)	8	9	4	7	6	6	4	1	45
Leptodea leptodon (Rafinesque, 1820)	1	-	-	-	-	-	-	-	1
Obliquaria reflexa (Rafinesque, 1820)	2	1	-	-	-	-	-	-	3
Obovaria olivaria (Rafinesque, 1820)	-	1	-	-	-	-	-	-	1
Potamilus alatus (Say, 1817)	4	6	4	3	4	1	-	1	23
Potamilus ohiensis (Rafinesque, 1820)	12	8	4	6	6	4	5	1	46
Pyganodon grandis (Say, 1829)	9	8	5	3	2	4	6	1	38
Quadrula quadrula (Rafinesque, 1820)	2	2	-	-	1	-	-	-	5
Toxolasma parvus (Barnes, 1823)	1	2	-	-	-	-	1	-	4
Truncilla donaciformis (Lea, 1828)	1	2	-	1	-	-	-	1	5
Utterbackia imbecillis (Say, 1829)	3	1	-	-	1	-	1	-	6
Total unionid species occurrences	54	46	20	21	26	16	22	8	213
Corbicula fluminea (Muller, 1774)	13	9	-	4	-	-	-	-	26
Total Species Occurrences	67	55	20	25	26	16	22	8	239
Total unionid species present	13	12	6	6	9	5	8	7	15
Total collection locales	15	10	6	8	11	9	10	2	71
Unionid species per locale	3.60	4.60	3.33	2.63	2.36	1.78	2.20	4.00	3.00

[a]Includes site 12 from Hoke (1983)
[b]Includes sites 7–11 from Hoke (1983)
[c]Includes site 6 from Hoke (1983)

Thomas Watters, Museum of Biological Diversity, The Ohio State University. All specimens were deposited at the Museum of Biological Diversity at The Ohio State University in Columbus, Ohio. The nomenclature in this paper follows Turgeon, *et al.* (1998). In addition, museums around the United States were visited to locate relevant recent and historic vouchers. These facilities are given in the acknowledgements section of this paper.

RESULTS

A total of 64 previously unreported sites are included in this study of the lower (channelized) Missouri River (Fig. 1). Survey work was conducted at 61 sites, and fifty-seven of these sites, or 95%, produced unionids. Only four sites were unproductive. The three additional new sites included in the study represent recent collections in museum holdings examined by the author. The remaining seven sites shown in Fig. 1 are from Hoke (1983).

The study area was divided into eight regions (Fig. 1). The first seven encompass 160-river km each, while the eighth includes the remaining 142-river km of the channelized Missouri River. Collection results at the 71 sites are summarized by region in Table 1, with 14 unionids and the exotic *Corbicula fluminea* in channelized reaches of the river and its floodplain. All species were collected as live, fresh dead, or recent shells from at least one locale, suggesting the fauna was extant at the time of collection.

The greatest species diversity was in regions I and II. The river in these regions is wider than in upstream regions and contains the greatest diversity of habitats. In addition, these regions were the most accessible, and consequently produced the greatest number of collection locales. The decrease in diversity in regions III through VIII is probably real, although possibly exaggerated due to more limited sampling. Species diversity was low and the number of unionid species per site ranged from one to eight, and averaged 3.0.

The most common species were *Leptodea fragilis*, *Potamilus ohiensis*, and *Pyganodon grandis*. Together these species accounted for 129 of the 213 unionid geographic occurrences, or over 60 percent of the total. *Leptodea fragilis* was the single most abundant unionid collected, although found at one site less than *P. ohiensis* (i.e. 45 vs. 46). *Leptodea fragilis* was most numerous in or near moderate current, but was less abundant in quiet water. The sole mussel recovered in the turbulent area beyond the tip of a wing dam was of this species. In contrast, *P. ohiensis* was more abundant in quiet waters, and most *P. grandis* were also found in sheltered habitats.

The native mussels *Anodonta suborbiculata* and *Potamilus alatus*, and the introduced *Corbicula fluminea*, were also relatively common. The five most common native mussels were recovered throughout the length of the channelized Missouri River. In contrast, in 1990 the distribution of *C. fluminea* was restricted to a reach of the Missouri River extending from the Mississippi confluence to a point immediately east of Kansas City, Missouri. Within that reach, the bivalve was usually abundant. Its absence from sites to the west suggests the species had not colonized the river beyond that point at the time of the collection.

Seven unionids were uncommon, together comprising only 38 (18%) of the 213 unionid geographic occurrences. *Lampsilis teres* and *Lasmigona c. complanata* were widely distributed but always

Table 2. Freshwater mussels (*Unionidae*) reported for the lower Missouri River and its floodplain from all published sources: L=live; F=fresh dead; R=recent; D=slightly to moderately weathered; W = weathered; S = chalky; X=present, condition not given.

	River				Lakes, Bayous & Sloughs			Ditches
	This Study							
SPECIES	Below Kansas City	Above Kansas City	Hoke (1983)	Simpson	This Study	Hoke (1983)	Utterback (1915–16)	Hoke (2005b)
Anodonta suborbiculata	F	R	F	-	L	D	X	R
Arcidens confragosus	-	-	-	-	-	-	X	-
Lampsilis teres	R	F	S	-	S	-	X	R
Lasmigona c. omplanata	R	R	L	-	W	-	X	R
Leptodea fragilis	L	F	L	X[a]	-	-	-	R
Leptodea leptodon	R	-	-	-	-	-	-	-
Obliquaria reflexa	R	-	-	-	-	-	-	-
Obovaria olivaria	L	-	-	-	-	-	-	-
Potamilus alatus	F	L	-	-	-	-	X	R
Potamilus ohiensis	L	F	L	-	W	-	X	R
Pyganodon grandis	F	F	L	X[b]	S	D	X	R
Quadrula quadrula	R	S	-	-	L	-	X	-
Toxolasma parvus	F	-	-	-	F	-	X	-
Truncilla donaciformis	R	R	-	-	-	-	-	-
Uniomerus tetralasmus	-	-	-	-	-	-	-	R
Utterbackia imbecillis	F	R	-	-	R	-	X	R
Total unionid species	14	10	6	2	8	2	10	9

[a]Simpson as cited by Utterback (1915–1916) - no reference given
[b]Simpson (1900)

infrequent. *Obliquaria reflexa*, *Quadrula quadrula* and *Toxolasma parvus* were more restricted in distribution, but similarly uncommon. In contrast, *Truncilla donaciformis* and *Utterbackia imbecillis* were on occasion quite abundant. *Utterbackia imbecillis* was most abundant in floodplain lentic habitats, while *T. donaciformis* was occasionally numerous in mixed rock, mud, and sand substrates along the main stem.

Two species were extremely rare. *Leptodea leptodon* and *Obovaria olivaria* were limited to one site each, and each by only a single specimen. *Leptodea leptodon* is federally endangered, and this specimen was reported in Hoke (1999). *Leptodea leptodon* is also reported from the unchannelized Missouri River along the Nebraska-South Dakota border (Hoke, 1983, Dugan, 2009).

All species were present in at least one Missouri River main stem collection locale. The fauna of detached floodplain lakes and sloughs was less diverse with only eight species, however, *Quadrula quadrula*, *Toxolasma parvus*, and *Utterbackia imbecillis* were more common in these lentic environments than in the Missouri River.

Unionids were generally absent from areas exposed to the strong currents of the lower Missouri River. Mussels were generally rare or absent in substrates subject to seasonal draw down, and when recovered from such areas were nearly always juveniles. Unionids were usually absent along rock-lined banks (revetments), but were occasionally plentiful when interstices had filled with sediment. In contrast, locales sheltered from strong currents almost always produced unionids, sometimes in large numbers. Most productive habitats were associated with stream control structures such as revetments and wing-dams. Mussels were also recovered from natural habitats along inside banks below sharp bends, and in substrates of natural rock and sediment.

Examination of museum collections revealed no pre-1938 specimens from the now-channelized reaches of the Missouri River, though several early, unpublished records were noted from the middle Missouri River, as well as from floodplain lakes within the study area. The former records are discussed in a later section. The Museum of Zoology at the University of Michigan holds previously unpublished vouchers of *Lasmigona c. complanata* (7718) and *Potamilus ohiensis* (7663) from Crystal Lake, a Missouri River oxbow in northeastern Nebraska. Vouchers supporting Utterback's (1915–1916; 1917) reports from Missouri River floodplain lakes in northwestern Missouri were also noted at a number of museums.

DISCUSSION

The unionid fauna from the current study is compared with that reported for channelized reaches of the Missouri River and its floodplain from all published sources in Table 2. All unionid species previously reported from the lower sector of the Missouri River were recovered and eight additional species are reported here. With two exceptions, the fauna obtained from floodplain habitats in this survey is identical to that given by Utterback (1917) for floodplain lakes. *Potamilus alatus* and *Arcidens confragosus* (Say, 1829), reported in the early study, were not recovered during the current survey. Since Utterback (1917) listed *P. alatus* as "scarce" in Missouri floodplain lakes, the failure to collect this mussel in similar habitats may be due to its rarity, however, *A. confragosus* was reported as "fairly abundant" in the same study. This species is unreported in the Missouri River Basin in Missouri after 1919 (Oesch, 1995) and is now extremely uncommon in the Missouri River Basin as a whole (Hoke,

2005b). *Arcidens confragosus* may have been extirpated from the channelized floodplain, though recently reported for the unchannelized reach above Ponca State Park (Perkins and Backlund, 2000). *Uniomerus tetralasmus* (Say, 1831), collected from floodplain ditches near the Missouri-Iowa border (Hoke, 2005b), was not recovered in this survey probably due to an absence of collection effort in similar floodplain habitats.

It is difficult to reconcile current sampling results for main stem habitats to early literature on the Missouri River. While unionids were recovered from almost every site in this survey, there are no vouchered early reports of unionid mollusks within the presently channelized reaches of the Missouri River main stem. Most early articles on the fauna of the middle and lower Missouri River report an absence of unionids and attribute this totally or in part to the sediment load of the river (Hayden, 1862; Over, 1915, 1942; Bartsch, 1916; Utterback, 1915–1916, 1917). Since there was a dramatic decline in turbidity following construction of the upper and middle Missouri River dams between 1938 and 1963 (SCJT, 1959; Sayre and Kennedy, 1978), it is possible the presence of mussels in the lower Missouri River represents a post-1938 colonization of a formerly uninhabitable environment.

This conclusion is based upon the validity of two premises: (1) early research sufficient to establish an absence of unionids prior to the closing of Fort Peck Dam in 1938; and (2) solid evidence that the sediment load of the historic Missouri River precluded the survival of all unionid species. Analysis of early publications, museum vouchers and recent research casts doubt on both premises.

Analysis of Pre-1938 Investigations of the Missouri River Unionid Fauna

There is no evidence thorough fieldwork on freshwater mussels was conducted in the pre-1938 lower Missouri River. In fact, only two individuals are known to have conducted any fieldwork on the mussels of the main stem of the middle and lower Missouri River: Hayden (1862) and Bartsch (1916), and neither study was comprehensive.

Hayden (1862) described the Missouri River as devoid of molluscan life below the confluence of the Milk River in central Montana due to turbidity. Since Hayden was investigating the geology and natural history of the entire Missouri basin above and including the Kansas Basin, it is unlikely he conducted a thorough mussel study. Bartsch (1916) apparently found nothing in an undocumented effort along the lower 13 to 16 kilometers of the Missouri River conducted during a portion of only one day, August 13, 1907 (Wilson, 1910).

Utterback (1915–1916) did collect *Pyganodon grandis* in sloughs and bayous along the Missouri River, but it is doubtful he collected in the main stem, for in refuting a report (attributed to Simpson) of *Leptodea fragilis* from the Missouri River, he did not rely upon personal experience, but referred to vague, unnamed sources: "no mussel life is actually reported for the main stem of this River throughout the State."

The thoroughness of early efforts in the middle Missouri River also does not inspire confidence. Coker and Southall (1915) state, "the Missouri River itself has been known to be without shell resources", but provide no citations in support. Since they did not sample in the Missouri River (Coker, 1919), it is unclear how they reached their conclusion. In reporting on the mollusks of South Dakota, Over (1915, 1942) did not document any effort in the Missouri River. His comments on the Missouri River may be general observations of the river, located a few kilometers south of his residence.

Some statements in the early literature support the view of a limited unionid fauna for the historic middle and lower Missouri River. Though Hayden (1862) reported an absence of mollusks below the Milk River confluence in eastern Montana, he contradicted his own report by listing *Lasmigona c. complanata*, as *Margaritana complanata* (Lea), at "Fort Clark, in Missouri", several hundred kilometers below the Milk River confluence in northwest North Dakota (Fig. 1). Lea (1858) reported the receipt of voucher specimens of *L. c. complanata* as *M. complanata* and *Lampsilis siliquoidea* as *Unio luteolus* (Lamarck) collected by Hayden from the Missouri River at Fort Clark, Nebraska Territory. Simpson (1900) includes the Missouri River in the distribution of *Pyganodon grandis*, and listed *Leptodea fragilis* for the river as well (Utterback, 1915–1916).

The author was unable to locate vouchers to document these citations, but it may be significant that three of these species were collected from the channelized Missouri River in the current study, and all are recently reported from reaches along the Nebraska - South Dakota border (Hoke, 1983, 2005a; Clarke, 1996; Perkins and Backlund, 2000; Schearer, et al., 2005). *Leptodea fragilis* and *Pyganodon grandis* were among the three most common species recovered in this study, and one would expect at least one of these species to be present in most samples collected today from sites in the lower Missouri River.

The conclusions of Hayden (1862) and Over (1915, 1942) on the absence of unionids from the middle Missouri River are contradicted by pre-1938 vouchers in collections at the U. S. National Museum (USNM) and the University of Colorado Museum of Natural History (UCMNH). These indicate that three unionid species inhabited the Missouri River in central South Dakota before 1938: *Lampsilis siliquoidea* (USNM 676897) in 1900, and *Potamilus ohiensis* (UCMNH 15116) and *Pyganodon grandis* (UCMNH 15117) in 1927. Mussels may have been uncommon in the middle Missouri River, but they were not absent entirely. Given the almost non-existent early collection effort in the lower Missouri River, unionids may have been present but undetected in that sector as well.

Support for unionid absence in the middle and lower Missouri River ultimately focused on the known deleterious impact of silt on unionids (Lefevre and Curtis, 1912; Ellis, 1937). Based upon the vouchers above, silt did not preclude the existence of some unionid species in the middle Missouri River in the early twentieth century, and its impact appears to be less complete than the early literature assumed.

Hayden (1862) probably over-estimated the impact of "turbidity" in reporting unionids to be absent from the Missouri River below the confluence of the highly turbid Milk River in eastern Montana. The Milk River was named for the milky appearance of its silt-laden waters. Though the waters of this stream still cloud those of the Missouri below their confluence (Schneiders, 1999), mussels were recently collected from the Missouri River below that point, and four unionid species were recovered from the Milk River as well (Gangloff and Gustafson, 2000). Mussels are also recently reported from reaches of the silty Yellowstone River, a major tributary of the Missouri, in southern Montana (Op. cit.).

The most influential proponent of unionid absence from the Missouri River was Bartsch (1916). He noted the mud content of the Mississippi below the Missouri River confluence, and a reported absence of mussels in the reach extending from the Missouri River confluence to the mouth of the Ohio River, to argue that mussels could not survive in the Missouri due to "the heavy load of mud" in its waters, and speculated mussels were "probably strangled" as a consequence.

Mud in suspension may have been prohibitive for many unionids, but it seems doubtful it would have precluded all unionid species. Ellis (1931) attributed the decline of many commercial mussels in the Mississippi to increases in silt, but noted two species, *Pyganodon grandis* and *Utterbackia imbecillis*, became more abundant in these conditions. Significantly, the former species is also one of the few reported for the historic lower Missouri River (Simpson, 1900).

There is also some question as to the validity of Bartsch's report of an absence of unionids in the Mississippi below the Missouri River confluence. Surveys conducted on the Mississippi in 1930 and 1931 recovered mussels in this reach of the Mississippi, "usually" in sloughs along the shore (Van Der Schalie and Van Der Schalie, 1950). Thus, while there seems little doubt that there was a drastic decrease in unionids in the Mississippi below the Missouri River, there is evidence that at least some mussels were present.

Bartsch's hypothesis was never critically reviewed or challenged. Over (1915) and Utterback (1915–1916) initially cited "velocity of current and rapid deposition of sediment" and "loess soil held in suspension together with ... shifting sand bars and mud beds" respectively, as rationales for the presumed absence of unionids. However, subsequent to Bartsch's publication, both concurred with Bartsch (Utterback, 1917; Over, 1942).

With the acceptance of Bartsch's hypothesis by these workers, research on Missouri River unionids, with only one exception, ceased for more than 60 years, and findings at variance with the faunal barrier hypothesis may have been dismissed. In 1927, Henderson published two vouchers (UCMNH 15116 & 15117) donated to the University of Colorado Museum of Natural History from a locale near Chamberlain, South Dakota, however, he failed to disclose their Missouri River origin, though this information is given in the related catalogue entries and written in the shells as well.

Unionid Habitat in the Lower Missouri River

The distributional patterns revealed in this study suggest mussels are generally restricted to limited portions of the Missouri River floodplain. The habitats occupied are characterized by slow to moderate currents, stable substrates, and are usually not subject to dewatering during periods of low flow. This suggests, the primary environmental parameters restricting unionid populations in the Missouri River are the direct and indirect impacts of the river's strong currents, and low winter water levels.

Historically, the Missouri River had strong currents, but with channelization of the lower river, average current velocity increased three fold (Schneiders, 1999). The primary effect of rapid currents for Missouri River unionids is in the destabilization of the river's sandy substrates. Sayre and Kennedy (1978) report "the bed of the river consists of moving sand waves and bars without quiet areas" and, as a result, the habitat of the main channel is a "submerged biological semi-desert." The general absence of unionids from unstable substrates has long been known (Baker, 1928; Murray and Leonard, 1962; Brim Box and Mossa, 1999). Holland-Bartels (1990) found juvenile unionids maintained position on sand sediments in slow currents, but were swept away by strong flows. Hoke (1994, 1995, 2005a) has attributed the general absence of unionids in most reaches of the Elkhorn, Platte, and Niobrara rivers in Nebraska to the prevalence of shifting sand substrates. Strayer (1999) and Gangloff and Feminella (2007) have noted a correlation between mussel beds and areas protected from current shear during floods, and Brim Box et al. (2002) suggest the need to explore the relationship between the location of mussel beds and protection from shear stress in Atlantic coastal drainages. The strong correlation of mussels with slow currents in this study is probably due to the related presence of stable substrates. When unionids were recovered from reaches with strong currents, they were almost always obtained from substrates where rock elements stabilize lighter sand and mud components.

Strong currents also impact freshwater mussel reproduction and dispersal in many main channel habitats due to their impact upon potential host fish. The life cycles of most unionid species require the infection and parasitic attachment of the larval form (ie. glochidia) to species specific host fish or salamanders where transformation to the juvenile form occurs. Host fish also constitute the primary means of unionid dispersal. In the channelized Missouri River, fish are highly concentrated in slow water habitats, and uncommon in the swift water of the main channel (Schneiders, 1999). In fact, the United States Department of the Interior (1980) reports that no fish species currently inhabits nor are any commonly found in the main channel of the lower Missouri River. Fish expend too much energy fighting the strong currents to remain in the channel for any appreciable period of time (Schneiders, 1999). It is likely that diminished host fish availability adversely impacts unionid reproductive efficiency and recruitment in most main channel habitats.

Low winter water levels also restrict current mussel populations. Flows are artificially lowered in the late fall due to suspension of barge traffic on the river, and remain at minimal levels until late March. Unionids must either move out of dewatered substrates or die of dehydration or exposure to freezing temperatures, thus explaining the general absence of mature shells from such substrates. The only exposed areas populated by mature specimens in this study were the lower 50 m of sandbar side channels along inside bends of the river. These habitats are populated during the spring and summer but, as waters recede in the fall, mussels move downstream into deeper waters, leaving scores of mussel tracks.

A third factor, silt, may restrict species diversity in some habitats. The presence of *Lampilis teres* and *Leptodea leptodon*, reported to be intolerant to silt (Brim Box and Mossa, 1999; Parmalee and Bogan, 1998), indicate silt levels in the channelized Missouri River are generally low. However, seven of the fourteen unionid species collected in this survey (*Anodonta suborbiculata*, *Leptodea fragilis*, *Obliquaria reflexa*, *Pyganodon grandis*, *Quadrula quadrula*, *Truncilla donaciformis*, and *Utterbackia imbecillis*) are reported to be tolerant to silt (Brim Box and Mossa, 1999), suggesting silt may currently be an important factor influencing species composition in some habitats. Pools below wing dams are presently the most common habitat for unionids in the lower Missouri River, and these pools are also by design, areas of silt deposition, possibly accounting for the abundance of silt tolerant species in the lower Missouri River.

Any analysis of unionid habitat in the historic lower Missouri River is conjectural, since no unionids were documented and little research was conducted, however, inferences on potential habitat can be deduced from observations made prior to channelization, coupled with a knowledge of natural habitats currently utilized. The available literature suggests that factors currently impacting unionids in the channelized Missouri River were also present and probably significant in the historic lower Missouri River.

The unchannelized lower Missouri River was known for turbidity, strong currents, and a shifting channel, and river substrates were primarily sandy. Pierce (1983) notes the historic lower Missouri River was essentially a braided stream below the Platte River confluence in Nebraska due to huge amounts of sand input from the Platte system. Strong currents and sandy

substrates undoubtedly produced unstable substrate conditions in the historic lower Missouri River.

The pre-1938 Missouri River carried a tremendous amount of sediment. The heavy sediment load coupled with often-swift currents fostered substrate and channel instability. During seasonal rises and other periods of high water, sediment from the river bottom was picked up and moved downstream until flows lessened, at which time the heavier elements were rapidly deposited on the riverbed surface, often to a depth of several feet (Over, 1915; Schneiders, 1999). This process promoted changes in the location of the river's channel. The heavy sediment load coupled with the high mobility of the sediment in the river doubtlessly precluded most unionid species, and adversely impacted most potential habitats, but these conditions would not necessarily preclude populations of silt tolerant species in sheltered habitats.

Due to the instability of the pre-1938 Missouri River channel, most specific habitats in the river were probably relatively short lived. In these conditions, thin-shelled, rapidly maturing unionids such as *Leptodea fragilis* and *Pyganodon grandis* would have a reproductive advantage over slower maturing, thicker shelled species. It is perhaps not coincidental these species were reported from the pre-1938 river (Simpson, 1900; Utterback, 1915–1916), and were among the most common mussels recovered in the current survey.

Low winter flows were also characteristic of the pre-1938 Missouri River and would likely have been even more significant for freshwater mussels than is true today, since the lower Missouri was, on average, three times as wide and correspondingly more shallow than the channelized river (Schneiders, 1999). Thus a much greater portion of the historic riverbed would have been dewatered in the winter and exposed to freezing temperatures. Viable unionid populations must have been largely restricted to substrates submerged during the minimal winter flow regimes.

Known productive historic floodplain habitats included sloughs, bayous, and detached lakes (Utterback, 1915–1916; 1917), all of which were far more extensive prior to channelization. Other potential habitats may have included attached lakes, backwaters, side-channels, and sheltered refugia in the main channel, such as those along inside banks below sharp bends in the river, and rare natural substrates composed of mixed rock, mud, and sand. Trees, brush and other debris washed from river banks and subsequently anchored in sediment (termed snags or embarrases on the Missouri River) may have sufficiently deflected currents from substrates immediately below to provide habitat for scattered populations of rapidly maturing unionid species. These environments did provide habitat for potential host fish in the pre-channelized river (Schneiders, 1999).

Due to an absence of early vouchers, it is not possible to completely reject the hypothesis that mussels were historically absent from the lower Missouri River. However mussel research was of insufficient quality to support this contention. Given the extremely limited collection efforts in the lower Missouri River before 1938, the absence of vouchers cannot be viewed as conclusive proof of a pre-1938 absence of mussels, but may reflect an absence of collection effort in the scattered slow water refugia that were the most favorable habitats for unionid populations. There is no compelling evidence to support the position that the suspended sediment load of the pre-1938 Missouri River precluded all unionids, though it almost certainly limited diversity in most habitats to silt tolerant species.

Current distributional patterns indicate unionids are present in substrates sheltered from the direct impact of strong currents, and further restricted by minimal winter flow regimes. I hypothesize a similar model of unionid distribution for the pre-1938 river, with unstable substrates and low winter flows precluding mussels from most substrata, viable habitats restricted to areas sheltered from strong currents, and the unionid fauna limited to silt tolerant species in most favorable habitats.

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LITERATURE CITED[1]

BACKLUND, D. C. 2000. Summary of current known distribution and status of freshwater mussels (*Unionoida*) in South Dakota. Central Plains Archeology 8:69–77.

BAKER, F. C. 1928. The fresh water Mollusca of Wisconsin. Part II. Pelecypoda. Bulletin of the Wisconsin Geological and Natural History Survey. University of Wisconsin 70(2):1–495.

BARTSCH, P. 1916. The Missouri River as a faunal barrier. Nautilus 30:92.

BLAND, T. and J. G. COOPER. 1861. Notice of land and freshwater shells collected by Dr. J. G. Cooper in the Rocky Mountains, etc., in 1860. American Lyecium Natural History, New York, vii, separate, pp. 1–9.

BRIM BOX, J. and J. MOSSA. 1999. Sediment, land use, and freshwater mussels: prospects and problems. Journal of the North American Benthological Society 18:99–117.

BRIM BOX, J., R. M. DORAZIO, and W. D. LIDDELL. 2002. Relationship between streambed substrate characteristics and freshwater mussels (Bivalvia: Unionidae) in coastal plain streams. Journal of the North American Benthological Society 21:253–260.

CLARKE, A. H. 1996. Final report, results of a biological survey for *Leptodea leptodon* (Rafinesque, 1820) in the Missouri River in southeastern South Dakota. A report prepared for the U. S. Fish and Wildlife Service (under contract no. 60181-2-1619), Ecosearch, Inc., 48 pp.

COKER, R. E. 1919. Fresh-water mussels and mussel industries of the United States. Bulletin of the U. S. Bureau of Fisheries 36 (1917–1918): 13–89, 46 pls. Issued separately as U.S. Bureau of Fisheries Document 865.

COKER, R. E. and J. B. SOUTHALL. 1915. Mussel resources in tributaries of the upper Missouri River. Report of the U. S. Commissioner of Fisheries for the fiscal year 1914. Appendix 4:1–17. Separately issued as Bureau of Fisheries Document No. 812.

COOPER, J. G. 1869. Notes on the fauna of the Upper Missouri. American Naturalist 3:294–299.

DUGAN, J. 2009. Game and Parks lists endangered mussel. Lincoln Journal Star. March 13, 2009.

[1] Two surveys on the unchannelized Missouri River above Ponca State Park were not made available to the writer and could therefore not be cited in this paper.

ECOLOGICAL SPECIALISTS, INC. (ESI). 1998, Final Report: unionid survey in Lake Sharpe, South Dakota and possible effects of drawdown. Submitted to U. S. Army Corps of Engineers, Omaha District, Omaha.

ELLIS, M. M. 1931. Some factors affecting the replacement of the commercial fresh-water mussels. U. S. Department of Commerce, Bureau of Fisheries. Fishery Circular No. 7, 10 pp.

ELLIS, M. M. 1937. Erosion silt as a factor in aquatic environments. Ecology 17:29–42.

GANGLOFF, M. M. and J. W. FEMINELLA. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, U.S.A. Freshwater Biology 52:64–74.

GANGLOFF, M. M. and D. L. GUSTAFSON. 2000. The freshwater mussels (Bivalvia: Unionoida) of Montana. Central Plains Archeology 8:121–130.

HAYDEN, F. V. 1862. On the geology and natural history of the Upper Missouri. Transactions of the American Philosophical Society 12:1–218.

HENDERSON, J. 1924. Mollusca of Colorado, Utah, Montana, Idaho and Wyoming. University of Colorado Studies 13(2): 65–223.

HENDERSON, J. 1927. Some South Dakota mollusca. The Nautilus 51:19–20.

HOLLAND-BARTELS, L. E. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. Journal of the North American Benthological Society 9:327–335.

HOKE, E. 1983. Unionid mollusks of the Missouri River on the Nebraska border. American Malacological Bulletin 1:71–74.

HOKE, E. 1994. A survey and analysis of the unionid mollusks of the Elkhorn River Basin, Nebraska. Transactions of the Nebraska Academy of Sciences 21:31–54.

HOKE, E. 1995. A survey and analysis of the unionid mollusks of the Platte Rivers of Nebraska and their minor tributaries. Transactions of the Nebraska Academy of Sciences 22:49–72.

HOKE, E. 1999. The scaleshell *Leptodea leptodon* (Rafinesque, 1820) in the Missouri River. Triannual Unionid Report 19:9.

HOKE, E. 2003. Investigations on the distributions of freshwater mussels in the Missouri River reservoirs of South Dakota. Final Report to South Dakota Department of Game, Fish and Parks, Pierre, South Dakota. 26 pp.

HOKE, E. 2005a. The freshwater mussels (*Mollusca*; *Bivalvia*; *Unionidae*) of northern Nebraska: The Missouri, Niobrara, and White River basins. American Malacological Bulletin 20:27–35.

HOKE, E. 2005b. The unionid mussels (*Mollusca*: *Bivalvia*; *Unionidae*) of Missouri River floodplain ditches in Fremont County southwestern Iowa and Atchison and Holt Counties northwestern Missouri. Journal of the Iowa Academy of Science 112:62–65.

LAFEVRE, G. and W. C. CURTIS. 1912. Studies on the reproduction and artificial propagation of fresh-water mussels. Bulletin of the U. S. Bureau of Fisheries, (30):105–201.

LEA, I. 1858. [Remarks on the Unionidae of Nebraska Territory, etc. Minutes of the March 23, 1858 meeting]. Proceedings of the Academy of Natural Sciences of Philadelphia, 10:13–14.

MURRAY, H. D. and A. B. LEONARD. 1962. Handbook of unionid mussels in Kansas. University of Kansas Museum of Natural History, Miscellaneous Publication, No. 28. 184 pp.

OESCH, R. D. 1995. Missouri naiades: a guide to the mussels of Missouri. Missouri Department of Conservation, Jefferson City, Missouri. 270 pp.

OVER, W. H. 1915. Mollusca of South Dakota. The Nautilus 29:79–81 and 90–95.

OVER, W. H. 1942. Mollusca of South Dakota. Natural History Studies, University of South Dakota 5:1–11.

PARMALEE, P. W. and A. E. BOGAN. 1998. The freshwater mussels of Tennessee. University of Tennessee Press, Knoxville. 328 pp.

PERKINS, K. and D. C. BACKLUND. 2000. Freshwater mussels of the Missouri National Recreational River below Gavins Point Dam, South Dakota and Nebraska. South Dakota Department of Game, Fish and Parks, SD GFP Report No. 2000-1, 24 pp.

PIERCE, D. 1983. Exploring Missouri River country. Missouri Department of Natural Resources, Division of Parks and Historic Preservation, Jefferson City. 276 pp.

SAYRE, W. W. and J. F. KENNEDY. 1978. Degradation and aggradation of the Missouri River. Proceedings of a workshop held in Omaha, Nebraska, 23–25 January 1978. Iowa Institute of Hydraulic Research Report No. 215, University of Iowa, Iowa City, Iowa. 61 pp.

SCHNEIDERS, R. K. 1999. Unruly River, two centuries of change along the Missouri. University of Kansas Press, Lawrence. 314 pp.

SHEARER, J., D. BACKLUND, and S. K. WILSON. 2005. Freshwater mussel survey of the 39-mile district – Missouri National Recreational River, South Dakota and Nebraska. Final Report. SD GFP Report 2005-008, 16 pp.

SIMPSON, C. T. 1900. Synopsis of the naiads or pearly fresh-water mussels. Proceedings of the U. S. National Museum 22:501–1044.

SIOUX CITY JOURNAL TRIBUNE (SCJT). 1959. "Muddy" no longer fits the Missouri. April 18, 1959.

STRAYER, D. L. 1999. Use of flow refuges by unionid mussels in rivers. Journal of the North American Benthological Society 18:468–476.

TURGEON, D. D., J. F. QUINN, JR., A. E. BOGAN, E. V. COAN, F. G. HOCHBERG, W. G. LYONS, P. M. MIKKELSEN, R. J. NEVES, C. F. E. ROPER, G. ROSENBURG, B. ROTH, A. SCHELTEMA, F. G. THOMPSON, M. VECCHIONE, and J. D. WILLIAMS. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks, Second Edition. American Fisheries Society Special Publication 26, 526 pp.

UNITED STATES DEPARTMENT of the INTERIOR. 1980, Missouri River Stabilization and Navigation Project, Sioux City, Iowa to Mouth. Detailed Fish and Wildlife Coordination Act Report. Fish and Wildlife Service, Field Office, Division of Ecological Services, North Kansas City, Missouri. 80 pp.

UTTERBACK, W. I. 1915–1916. The naiads of Missouri. The American Midland Naturalist 4:41–53; 97–152; 182–204; 244–273 (1915); 311–327; 339–354; 387–400; 432–464 (1916).

UTTERBACK, W. I. 1917. Naiadgeography of Missouri. The American Midland Naturalist 5:26–30 + folding chart.

VAN DER SCHALIE, H. and A. VAN DER SCHALIE. 1950. The mussels of the Mississippi River. The American Midland Naturalist 44:448–466.

WILSON, C. B. 1910. Dragonflies of the Mississippi valley collected during the pearl mussel investigations on the Mississippi River, July and August, 1907. Proceedings of the U. S. National Museum, Vol. 36, No. 1692, pp. 653–671.