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A re-examination of the endangered Higgins eye pearlymussel *Lampsilis higginsii* in the upper Mississippi River, USA

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ABSTRACT: We used our extensive data on freshwater mussels (Family: Unionidae), collected from 1984 to 2005 at multiple sites in the upper Mississippi River (UMR), USA, to examine the status of the endangered Higgins eye pearlymussel *Lampsilis higginsii* (Lea, 1857). Historically, this species inhabited an 850 km reach of the Mississippi River from Prescott, Wisconsin to Louisiana, Missouri, plus 9 UMR tributaries. After 1965 its range in the UMR declined by 50% and it was found in only 2 tributaries, the St. Croix and Wisconsin rivers. In river reaches unaffected by zebra mussels *Dreissena polymorpha*, *L. higginsii* mean density ranged from 0.0 to 1.4 m^{-2} (average = 0.25 m^{-2}) and it comprised less than 2% of the unionid fauna. Recent distribution and abundance data indicate that the range of *L. higginsii* populations was misrepresented on historical maps and suggest that populations were in fact either absent or very uncommon both at the periphery of their historical range and in small tributaries where they were reported historically. Although this species has always been rare, it can usually be found in appropriate habitats within its current range. It was listed as endangered before there were data on its density, recruitment, and relative abundance. Although it was nearly extirpated by *D. polymorpha* in the late 1990s, *L. higginsii* appears to be resilient to zebra mussel infestations. A multi-agency conservation plan is now being implemented to reintroduce this species into small and medium-sized rivers within and outside its historical range. Our data indicate that this species is not in imminent danger of extinction, has always been rare, and is not adapted to small rivers. It would be more realistic, and beneficial to *L. higginsii*, to implement strategies that protect all unionid species and the habitats upon which they depend.

KEY WORDS: Endangered Species Act · Upper Mississippi River · *Lampsilis higginsii* · Zebra mussels · Freshwater mussels · Unionidae

INTRODUCTION

In 1976, 3 yr after the Endangered Species Act (ESA) was implemented, 24 species of freshwater mussels (Family: Unionidae) were listed as endangered in the USA (41 Federal Register 24062-24067). During the intervening 30 yr many more mussel species were listed; 62 are now endangered and 8 are threatened (US Fish and Wildlife Service [USFWS] 2006). Of the 297 mussel species in the USA, 24% (Williams et al. 1993) are now protected by the ESA. Because of their relative immobility, reliance on stable substratum, clean water, suspended organic particulate matter for nutrition, and one or more host fish species for successful reproduction (Strayer et al. 2004), many aquatic ecologists consider freshwater mussels to be particularly vulnerable to anthropogenic impacts.

One of the 24 mussel species listed during 1976 was the Higgins eye pearlymussel (*Lampsilis higginsii* (Lea, 1857), sometimes spelled *higginsi*). Individuals of this species are moderately thick-shelled, yellow or brown, often green-rayed, with a maximum length of 10.2 cm (Cummings & Mayer 1992). They are currently found in the upper Mississippi River (UMR) between La Crosse, Wisconsin and Muscatine, Iowa as well as 2 tributaries, the St. Croix (Hornbach 2001; Wisconsin Department of Natural Resources [WDNR] 2004) and Wisconsin rivers (Havlik 2003, Heath 2003).

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Two recovery plans have been prepared for *Lampsilis higginsii.* The first (USFWS 1983) included a brief analysis of its historical and present distribution, ecology, life history, reasons for decline, and threats to its continued existence. Six locations in the UMR and one in the St. Croix River were identified as 'essential habitats' because they supported viable reproductive *L. higginsii* populations. Areas were considered to be non-essential if adults or shells were found, but there was no evidence of recent recruitment.

On 15 May 2000, the USFWS sent their 'Biological opinion' for the operation and maintenance of commercial navigation to the US Army Corps of Engineers (USACE) (USFWS 2000). The USFWS concluded that commercial navigation vessels would continue to jeopardize *Lampsilis higginsii* because they facilitated the spread of *Dreissena polymorpha* into river reaches that supported native mussels. High-density infestations of *D. polymorpha* (>1000 m^{-2}) can interfere with the ability of native mussels to feed and reproduce and have caused substantial mortality (Ludyanskiy et al. 1993, Schloesser et al. 1997, Ricciardi et al. 1998). The 'Biological opinion' recommended that the USACE develop methods to recover *L. higginsii*, and biologists from both agencies developed conservation tactics that were described in a subsequent recovery plan (USACE 2002). A key component of the plan was to re-establish *L. higginsii* in 7 rivers inside and 8 rivers outside its historical range.

The second recovery plan (USFWS 2004) was more extensive than the first and referred to essential habitats as Essential Habitat Areas (EHA). It identified 3 locations in addition to those in the first plan — 1 in the Wisconsin River and 2 in the St. Croix River. The second plan considered sites to be essential if *Lampsilis higginsii* comprised at least 0.25% of the mussel fauna, the assemblage was dense (>10 m^{-2}) and contained at least 15 species, each >0.01 m^{-2}. The plan recommended monitoring to assess status and indicated that *L. higginsii* would be downlisted to 'threatened' if populations in 5 EHAs were 'reproducing,' 'self-sustaining,' and 'not threatened by zebra mussels.' It would be delisted if populations in 5 EHAs were 'reproducing,' 'self-sustaining,' 'not threatened by zebra mussels,' and were 'sufficiently secure to assure long-term viability.' As an example of recovery efforts, the plan contained a list of 37 sites in 7 rivers (UMR, St. Croix, Wisconsin, Wapsipinicon, Cedar, Iowa, and Black) where *L. higginsii* had been recently released (2000 to 2003).

Lampsilis higginsii was listed as endangered and the essential habitat concept was developed before there were quantitative data on its relative abundance and density. In the late 19th and much of the 20th century most investigators collected live mussels and shells from shallow water and shoals by hand. Before diving became commonplace, the best access to deep water was with a commercial device known as the brail, a 2.7 to 5.4 m-long metal or wooden bar with 4-pronged metal hooks attached with short chains. Brailing is a biased qualitative method and has an efficiency of about 1% (Thiel 1981). Divers were not used in the UMR for scientific mussel surveys until the late 1970s and early 1980s (Havlik 1978, Fuller 1980, Thiel 1981) after *L. higginsii* was listed and only a few years before the first recovery plan was prepared.

Recent information on mussels obtained using divers and other improved methods provide an opportunity to re-examine the status of freshwater unionid species such as *Lampsilis higginsii*. Here, we discuss our data on freshwater mussels and *L. higginsii*, based on quantitative and qualitative sampling using divers from 1984 to 2005 at 15 locations in the UMR. In addition, we examine the historical distribution and abundance of *L. higginsii*, its recovery plans (USFWS 1983, 2004), and difficulties of monitoring a species that is both rare and endangered. Our purpose is to use this information to examine the status of *L. higginsii* and to comment on recently implemented conservation tactics designed to increase its range. Data for this paper came from our own research and other published studies and interpretation partly based on insight gained by A. C. Miller while serving on the Higgins Eye Recovery Team, 1984 to present.

MATERIALS AND METHODS

We collected mussels with a combination of qualitative and quantitative methods using a 6-person dive crew equipped with surface-supplied air, communication equipment, and a pneumofathometer to measure water depth. Qualitative samples were obtained by having a diver conduct an unconstrained, timed search over a fairly restricted area of the bed while retrieving all mussels encountered by touch. Live mussels were taken to shore, identified and counted but not measured, since this method is biased toward larger-sized individuals. Qualitative sampling provides information on presence/absence, relative species abundance, and species richness.

Quantitative sampling was accomplished by having a diver retrieve all substratum, including dead shells, sand, gravel, and live mussels from the confines of a 0.25 m^2 aluminum quadrat. Substratum was placed in a 20 l bucket and transported to shore for processing. Contents of the bucket were sieved through a graduated screen series (minimum grid size = 6 mm) and all live mussels were removed, identified, and total shell length measured. Total substratum quantitative samples provide data on density and population structure since they are less size-biased than qualitative methods. *Dreissena polymorpha* were sampled using a 0.0625 m^2 quadrat. More information on sampling freshwater mussels can be found in Miller & Payne (1998) and Strayer & Smith (2003).

These data were obtained from sites along the UMR at River Mile (RM): 709, 655, 642, 635, 618, 612, 608, 571, 556, 505, 492, 485, 471, 456, and 450. Sites at RM 655, 642, 635, 618, 505, and 485 were those identified as essential in the UMR in the first recovery plan (USFWS 1983) (Table 1). We also sampled at RM 0.34 in the St. Croix River, an essential site identified in the first recovery plan (USFWS 1983). Two of the essential sites in the St. Croix River (RM 0.34 and 17.6) are in a lentic reach and the third is in a lotic reach at RM 50.2. The lentic reach is the lower 40 km, which is a 0.5 to 2.3 km-wide natural impoundment that used to be an arm of Lake Pepin (Hutchinson 1975) and is known as 'St. Croix Lake.' Information on mussels at upriver sites was taken from the WDNR (2004).

Studies were conducted for multiple sponsors to meet various objectives; therefore, years were not consecutive. The most extensive sampling was the EHA at RM 635 near Prairie du Chien, Wisconsin that includes 17 nearly consecutive years. This location, a secondary channel with slightly reduced discharge, has long been recognized by locals and experts as providing high-quality mussel habitat. Negative effects of zebra mussels on native species were not notable until after 1996; therefore, we analyzed pre- (1984 to 1996) and post- (after 1996) infestation data separately.

We obtained background information on the biology, ecology, and distribution of *Lampsilis higginsii* from Havlik (1980), and the 2 recovery plans (USFWS 1983, 2004). Havlik (1980) examined the pre- and post-1965 distribution of *L. higginsii* based on specimens and records obtained from the United States National Museum, American Museum of Natural History, and museums in Illinois, Minnesota, and Ohio. Havlik separated information into these 2 time periods because early 20th century data were sparse and 1965 marked the beginning of more detailed studies on *L. higginsii* (Marion Havlik, pers. comm.). Most of the distributional information on *L. higginsii* in the first recovery plan (USFWS 1983) was based on the paper by Havlik (1980).

Table 1. Areas identified as essential for *L. higginsii.* M: Main channel, S: Secondary channel (USFWS 1983, 2004)

River	Mile	City/State	Habitat
St. Croix	0.34	Prescott, WI	M
	17.6	Hudson, WI	M
	50.2	Franconia, WI	M
Wisconsin	48	Orion, WI	M
Mississippi	655	Lansing, IA	M
	642	Harpers Ferry, IA	M,S
	635	Prairie du Chien, WI	M,S
	618	Guttenburg, IA	M,S
	505	Cordova, IL	M
	485	Moline, IL	S

RESULTS

Between 1984 and 1996, total mean unionid density at the EHA located at RM 635 ranged from 29 to 150 individuals m^{-2} (Fig. 1). Differences were due to local periods of recruitment and mortality, as well as spatial variability. Zebra mussels were first observed at this site in 1992 and their mean densities increased rapidly each year, approaching 10 000 m^{-2} in 1996. We did not observe measurable effects on unionid mortality for 6 yr, until 1998 when total mean mussel density declined to approximately 10 m^{-2}. After 1995, large and small unionids were typically heavily encrusted with zebra mussels. They were alive, but obviously stressed. In 1999, zebra mussel density exceeded 10 000 m^{-2} and unionid density was less than 2 m^{-2}.

Prior to zebra mussel infestations (1984 to 1996) *Lampsilis higginsii* typically comprised less than 2% of the unionid assemblage at both essential and nonessential sites in the UMR (Fig. 2). Although total mussel density in the St. Croix River was substantially lower than in the Mississippi River, *L. higginsii* relative abundance was similar at both locations. In the UMR *L. higginsii* density ranged from 0.0 to 1.4 m^{-2} (average = 0.25 m^{-2}) at EHAs and was slightly less, 0.0 to 0.3 m^{-2} (average = 0.05 m^{-2}) at nonessential sites. Over this large temporal and spatial scale the relationship between total unionid density and *L. higginsii* percent abundance was not significant ($r = 0.126$, total $N = 59$). *L. higginsii* was routinely collected at RM 635 through 1996. From 1999 through 2003 none were collected, although it is likely that some were present but so rare they were not found.

The mussel assemblage at RM 635 began to recover from the zebra mussel infestation by 2005, when *Dreissena polymorpha* density declined to 250 m^{-2} (Mussel Coordination Team 2005). During that year 18 live unionid species were collected, and total mean density was 34.6 m^{-2}. Fourteen species, including *Lampsilis higginsii*, included individuals less than 30 mm long and therefore exhibited evidence of recent recruitment. The percentage of species exhibiting evidence of

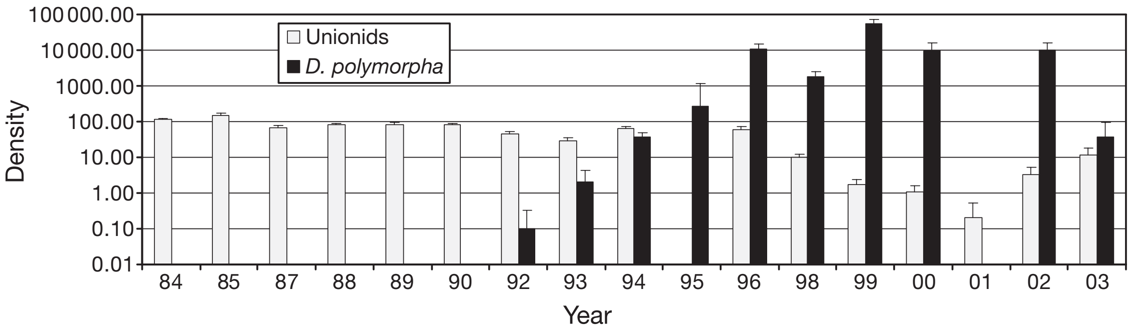

Fig. 1. Mean density + SE of unionids and *Dreissena polymorpha*, 1984 to 2003 in the secondary channel west of Prairie du Chien, River Mile (RM) 635.4, upper Mississippi River (UMR)

recent recruitment in 2005 (78%) was greater than any value (36.8 to 67%) we obtained from 1984 to 1996. During 2005, *L. higginsii* mean density and relative abundance was 0.8 m^{-2} and 1.9%, respectively, which was similar to pre-infestation values.

Relative abundance of *Lampsilis higginsii* increased slightly relative to other unionid species after 1996 (Fig. 3). This was mainly due to rapid and nearly total mortality of juvenile and sub-adults of common species such as *Amblema plicata*, *Obliquaria reflexa*, and *Quadrula* spp. Large individuals (virtually all *L. higginsii* that we collected were adults) then comprised a greater component of the assemblage. From 1984 to 1996 at essential habitats, *L. higginsii* comprised 0.59% (range = 0.0 to 1.7%) of the fauna. After 1996, when zebra mussel effects on unionid mortality were apparent, *L. higginsii* comprised 1.9% of the assemblage (range = 0.0 to 11.1%). Although overall relative abundance of *L. higginsii* increased at highly infested beds, total mean density declined. After infestation, total mean *L. higginsii* density was 0.08 m^{-2} (maximum = 0.8 m^{-2}), whereas prior to infestation it was 0.25 m^{-2} (maximum = 1.4 m^{-2}).

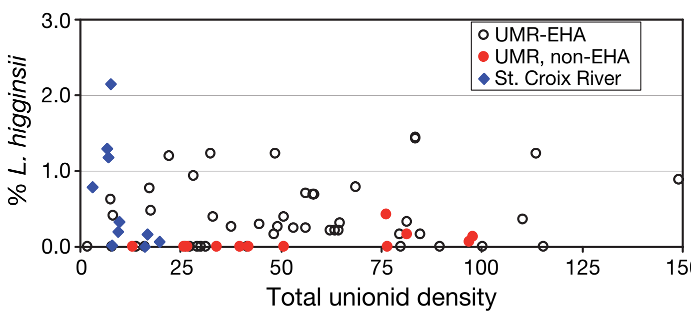

Fig. 2. The relationship between *Lampsilis higginsii* abundance and total unionid density (m^{-2}) at UMR Essential Habitat Areas, EHA (near RM 635 and RM 505) and nonessential habitats (near RM 709, 612, 608, 571, 556, 492, 485, 471, 456, and 450) 1984 to 1996. Density and *L. higginsii* abundance data from the St. Croix River at RM 17.6 (1988, 2000, and 2004) and at RM 50.2 (1988, 1996, 2000, and 2004) were taken from WDNR (2004)

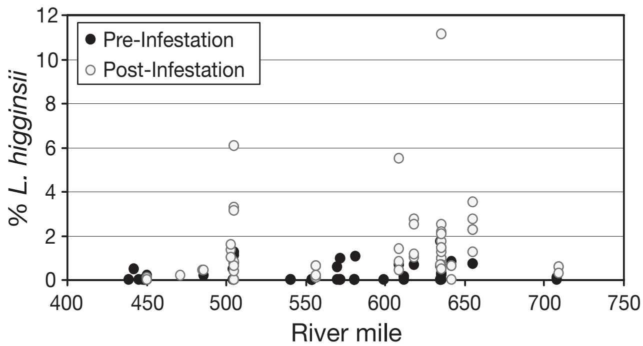

Fig. 3. Relationship between river mile and *Lampsilis higginsii* abundance at 15 locations in the UMR, 1984 to 1996 (pre-infestation) and 1997 to 2005 (post-infestation)

DISCUSSION

Abundance and distribution of *Lampsilis higginsii*

Although abundance data on *Lampsilis higginsii* prior to the 1980s are not complete, a review of historical information indicates that it was always rare. For example, in a study of archeological middens in southern Wisconsin, Theler (1987) identified 28 unionid species and found that *L. higginsii* comprised 0.10% of a sample containing more than 13000 individuals. Havlik & Marking (1980) examined over 17000 mostly relic shells from a secondary channel at RM 635 and reported that *L. higginsii* comprised 0.52% of the sample. In 1930 to 1931 Max Ellis collected mussels along a 1100-km reach of the UMR between Cairo, Illinois, and Point Au Sable, Minnesota (results were summarized by van der Schalie & van der Schalie 1950). Ellis collected nearly 7000 live mussels, identified 39 species, but found only 3 live *L. higginsii*. These abundance values are not substantially different from those at sites in the UMR prior to zebra mussel infestations.

Lampsilis higginsii density at sites in the UMR cannot be estimated prior to the 1980s. Regardless, information from recent sampling can be used to make inferences about historical density. Total mean unionid density at the majority of our sites in the UMR was less than 100 individuals m^{-2} (Fig. 2). Therefore, since this species typically comprises less than 2% of the native mussel fauna it is unlikely that high-density *L. higginsii* populations (i.e. greater than 5 m^{-2}) ever existed. Regardless, just because a species constitutes a small percentage of the fauna does not mean that existing population size at any one site is small. For example, Hornbach et al. (1995) estimated that there were 4000 live *L. higginsii* in the St. Croix River at RM 50.2, and as many as 260 000 at RM 17.6. Miller & Payne (1997) estimated that the number of *L. higginsii* at EHAs in the UMR ranged from several thousand to more than 500 000. Wilcove et al. (1993) reported estimates of the number of living individuals present when various species were placed on the endangered species list. The median number of living specimens of threatened and endangered invertebrate species was 4161 and 515 individuals, respectively, when listed. These values are substantially lower than recent estimates of living *L. higginsii* in the UMR.

In comparison with the mainstem Mississippi River, the EHAs in the St. Croix and Wisconsin rivers support low-density unionid populations, regardless of the fact that they are high-quality habitats. For example, total mean unionid density at RM 50.2 and 17.6 in the St. Croix River was 9.5 to 19.7 m^{-2} and 6.6 to 7.5 m^{-2}, respectively (Hornbach et al. 1995, WDNR 2004). Relative abundance of *Lampsilis higginsii* was slightly higher (1.2 to 2.2%) at the lentic site (RM 17.6) than at the lotic site farther upriver (0.0 to 0.33%). Mean unionid density at the EHA in the Wisconsin River in 1998, 1995, and 2002 was 6.05, 2.52, and 1.34 m^{-2}, respectively (Heath 2003). A single live *L. higginsii* (0.34% of the assemblage and 0.02 m^{-2}) was collected in 1988, and none was taken during the other 2 study years. In comparison with the Mississippi River proper, *L. higginsii* was much less abundant in those tributaries.

The pre-1965 range of *Lampsilis higginsii* was from Prescott, Wisconsin (RM 811) to Louisiana, Missouri (RM 283), a distance of 850 km (Havlik 1980). In addition to the mainstem Mississippi River, historical records included 9 tributaries: the Minnesota River, Minnesota, the St. Croix and Wisconsin rivers, Wisconsin, and the Rock, Illinois, and Sangamon rivers, Illinois. In Iowa there were records of *L. higginsii* in Wapsipinicon River, Iowa River, and a tributary, the Cedar River (Fig. 4).

An examination of distribution maps suggests that *Lampsilis higginsii* declined substantially after 1965 (Fig. 4). After 1965, 196 and 248 km were lost from the northern and southern part of its range, respectively; an overall decline of more than 50% (Havlik 1980). Currently this species is reported from Pool 17, which begins at Lock and Dam 17 near RM 437, to Pool 7, which ends at Lock and Dam 6 near RM 714. Some losses can be readily explained; virtually all mussels were eliminated from a river reach south of St. Paul by domestic and industrial pollution in the mid-19th

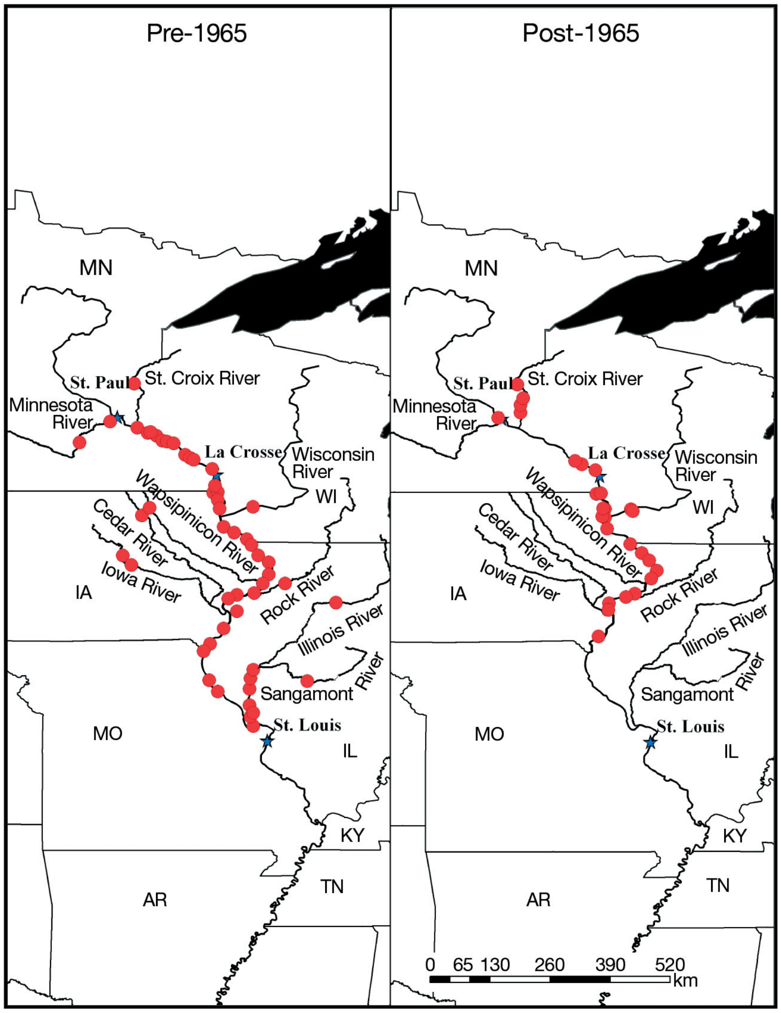

Fig. 4. Pre- and post 1965 distribution of *Lampsilis higginsii*, based on Havlik (1980) and USFWS (2004). For the post-1965 map the *L. higginsii* record for the Wisconsin River was included, although it was inadvertently omitted from maps in both recovery plans (USFWS 1983, 2004); several shell records from outside the historical range of (Cawley 1996), and discussed in the second recovery plan (USFWS 2004), were not included

Table 2. Mean annual discharge (m^3 s^{-1}) in the mainstem upper Mississippi River (UMR) and near mouths of tributaries where *L. higginsii* is currently and was historically found

River	Location	Mean annual discharge	Years of record
Mississippi	Prescott, WI	1292	76
	Winona, MN	1819	77
	Clinton, IA	2501	132
Illinois	Valley City, IL	1015	66
Wisconsin	Muscoda (near Orion), WI	509	91
Iowa River	Wapello, IA	366	91
St. Croix	St. Croix Falls, WI	321	99
Rock	Joslin, IL	298	65
Cedar	Conesville, IA	274	66
Minnesota	Ft. Snelling St. Park, MN	199	3
Sangamon	Oakford, IL	175	77

century (Anfinson 2003, Fremling 2005). Some unionid species have recently been collected and this river reach is recovering (Kelner & Davis 2002). In addition, *L. higginsii* was extirpated by pollution from the Illinois River (Mills et al. 1966, Starrett 1971), although some unionid species have recovered (Sietman et al. 2001).

Both recovery plans (USFWS 1983, 2004) suggest that its reduced range could be attributed to anthropogenic impacts, including increased sedimentation, river modifications, and poor water quality. Loss of fish hosts has been cited as problem for native mussels (Williams 1993, Strayer et al. 2004); however, Waller & Holland-Bartels (1988) identified 4 hosts for this species (*Micropterus salmoides, M. dolomieu, Stizostedion vitreum vitreum* and *Perca flavescens*), which are common in the UMR. Although virtually all rivers were affected by anthropogenic disturbances in the 19th and 20th centuries, we have found no specific event that eliminated *Lampsilis higginsii* from the downstream reach of the LMR and the other tributaries.

Historical data do not provide clear evidence that stable, recruiting *Lampsilis higginsii* populations existed in the 7 tributaries where it has not been collected recently. For example, there are no records of live specimens in the Minnesota River. Dawley (1947) reported one shell, but this was later determined to be *Obovaria olivaria* (Bright et al. 1990). M. E. Havlik (unpubl. reports) found *L. higginsii* shells, and Bright et al. (1990) found what they referred to as a 'probable' *L. higginsii* shell in the Minnesota River. Although *L. higginsii* was reported from the Iowa River, Frest (1987) did not find relic shells during an extensive survey. The reports from the Rock, Sangamon, Cedar, and Wapsipinicon rivers date from the 19th or early 20th century and consisted of one or a few specimens (Havlik 1980).

The historical distribution of *Lampsilis higginsii* includes tributaries with a wide range in average mean discharge (Table 2); however, recruiting populations now inhabit rivers with mean annual discharge greater than 500 m^3 s^{-1}. The only waterbody in Table 2 with mean annual discharge less than 500 m^3 s^{-1} that supports *L. higginsii* is the St. Croix River; however, as described above, the lower 40 km is impounded and functions like a higher order river. These data suggest that *L. higginsii* inhabits large rivers, not small tributaries.

Our data indicate that *Lampsilis higginsii* is slightly more abundant in the center than in the periphery of its range (Fig. 3). This is partly due to the presence of historically noteworthy high-quality beds at RM 655, 642, 635, 618, and 505, which supported high-density mussel assemblages. However, it is also likely that *L. higginsii* populations were always smaller at the northern and southern edge of its range because the river is slightly more erosional and less suitable for mussels north of La Crosse (RM 702.5) and south of Keokuk, Iowa (RM 364) (see Fig. 1 in Chen & Simons 1986). Erosional reaches of large rivers are slightly less suitable for unionids than more depositional sections (Layzer & Madison 1995). These organisms become increasingly scarce in the Mississippi River south of St. Louis, Missouri, and are absent in the river south of Memphis, Tennessee. Likewise, upper reaches of tributaries are typically less suitable than lower reaches for bivalves (Vannote et al. 1980). The observation that *L. higginsii* was more abundant in the downstream impounded reach of the St. Croix River than in the upstream, more lotic reach, further substantiates this. In the UMR it is possible that recruiting *L. higginsii* populations either did not exist or were very uncommon in the Mississippi River south of Muscatine and the upper reach near St. Paul.

Lampsilis higginsii recovery plans

In the original recovery plan (USFWS 1983) it was stated that only 3 live *Lampsilis higginsii* had been collected since 1932 and that viable reproductive populations had not been found recently. For this reason, the USFWS concluded that *L. higginsii* was in imminent danger of extinction and placed it on the endangered species list. This statement was then qualified by noting that there had been several extensive mussel surveys in the UMR since it was listed and that, 'Numerically *L. higginsi* may be less rare today than previously thought, but in all probability this reflects significantly greater collecting effort and the ability of a larger number of collectors to identify it.'

Our studies indicate that *Lampsilis higginsii* is primarily a large-river species, has always been rare, and successfully recruits at multiple sites along several hundred km of the UMR. There is little other evidence that small tributaries provide appropriate habitat for this species. It has always been rare and difficult to collect and was listed as endangered before there were adequate data on its distribution and abundance. Therefore, it is not surprising that recent population observations do not entirely confirm earlier assumptions.

Conservation measures

The second recovery plan (USFWS 2004) is explicit about the requirement to monitor beds with *Lampsilis higginsii* present; nonetheless, temporal change in density, recruitment, and mortality cannot be assessed accurately without an almost impossibly large sample set. Because of high variance-to-mean ratio, the number of quantitative samples needed to estimate density of rare species can be unreasonably high (see Green 1979). Results of our studies and those by the WDNR (2004) indicate that the number of 0.25 m^2 quadrats needed to reliably estimate *L. higginsii* density can exceed several thousand. Regularly collecting this many quantitative samples to meet such a goal could be more stressful than anthropogenic impacts. On the other hand, it makes little sense to design monitoring without sufficient replication to reliably assess trends. A potential solution would be to study a common surrogate species and apply results to *L. higginsii*. This could be accomplished with far fewer samples, and if adequately designed, should obtain some *L. higginsii* although not enough to reliable assess density or recruitment.

Mussel translocations, even when organisms are taken to suitable habitats within their range, are not always successful (Cope & Waller 1995, Miller & Payne 2006). There are several reasons not to translocate *Lampsilis higginsii* out of its current range. First, an examination of its distribution and abundance indicates that it is a large-river species and probably does not survive well in smaller tributaries. Second, although it is negatively affected by zebra mussels, *L. higginsii* is resilient to infestations and there is evidence that it can recover. Finally, conservation plans should recognize that this species has always been rare.

Endangered and threatened species share characteristics that make them vulnerable to extinction (Ehrlich & Ehrlich 1981). Such traits can include large size, low reproductive output, unique habitat requirements, limited geographic distribution, high economic or commercial value, or extreme rarity. Although by itself rarity could cause extinction (Arita et al. 1990), this is an ecological characteristic that defines relationships among distribution, abundance, and biological attributes (Rabinowitz 1981, Gaston 1994), which does not imply incipient extinction (Slobodkin 1986, Burke & Humprey 1987). Rare species are spatially restricted (not widespread) but common in the few places they occur, or widespread but uncommon where they occur (Gaston 1994), or both spatially restricted and uncommon. Presumably, the third combination would put a species most at risk of extinction. In the UMR, *Lampsilis higginsii* is widespread (occurs along several hundred km) and uncommon. An understanding of whether a species is rare and likely to become extinct, as opposed to being rare and temporally stable, should be considered not only when a species is listed, but when conservation actions are planned. Although the desire to protect very uncommon species is laudable, this would be a case of promoting conservation priorities (deciding which species should be protected) rather than conservation status (estimating the risk of extinction) (de Grammont & Cuaron 2006). The ESA should protect species because they might become extinct, not because they are rare.

Since the ESA was implemented, 302 and 1009 species have been listed as threatened and endangered in the USA, respectively (USFWS 2006). In the past 30 yr 42 species have been delisted; 16 had recovered (i.e. are no longer endangered) and 26 were either listed erroneously or determined later to be extinct. Certainly one strength of the ESA lies in the option to delist species when appropriate (Gerber 2003), although this is unlikely to happen (also see Mann & Plummer 1995).

Golly (1993), Worster (1994), and Reuss (2005) described the gradual shift in the late 20th century away from individual and population level studies toward more holistic approaches. The heavy emphasis on species protection in the early 1970s is giving way to concerns over ecosystem sustainability and societal needs (Cairns 2003). This does not mean that the ESA should be replaced by an ecosystem protection act (Salwasser 1991); the existing legislation already encourages ecosystem protection (Snape & Houck 1996). *Lampsilis higginsii* can be best protected by implementing conservation strategies that safeguard rich and diverse mussel assemblages and the habitats upon which they depend.

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