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Status of the freshwater mussel (Unionidae) communities of the mainstem of the Leon River, Texas

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ABSTRACT

1. The Leon River drainage, located in the Brazos River basin, has not been extensively surveyed for freshwater mussels (Family Unionidae). This is problematic given that three state-threatened species, *Quadrula houstonensis*, *Quadrula mitchelli*, and *Truncilla macrodon*, have historically occurred in this drainage and two are now candidates for protection under the US Endangered Species Act.

2. Mussels were sampled qualitatively at 44 sites in the summer and fall of 2011 to determine whether these species were still extant in the Leon River. The distributions and abundances of species at present considered common were also examined. Shell length data were assessed to determine the overall viability of the mussel fauna within the Leon River drainage.

3. In total, 2081 live mussels were collected representing 12 species, including the federal candidate species *Quadrula houstonensis*, but *Lampsilis hydiana*, *Quadrula mitchelli* and *Truncilla macrodon* were not collected. Overall mussel abundance and species richness was low and community composition was highly fragmented with riverine species largely occurring in the middle portion of the Leon River. There was evidence that population recruitment is occurring, but only for a few species.

4. River impoundment, inadequate instream flows, and agricultural practices are probable causes of the changes in mussel species composition. Further studies are needed to evaluate the impacts of reservoir releases on mussel persistence within this basin and in areas where droughts and low stream flow are commonplace. More information is needed on how agricultural practices affect mussel communities; the information that is currently available does little in the way of identifying factors that can be managed at site or reach scales. Studies that address these knowledge gaps will help resource managers to design more effective strategies to protect mussel populations within and outside this basin.

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KEY WORDS: river; rare species; distribution; land-use; invertebrates; drought; impoundment; agriculture; Unionidae

INTRODUCTION

North America contains the highest diversity of freshwater mussels (Bivalvia: Unionidae) in the world, with approximately 297 species occurring in the USA (Williams *et al.*, 1993). Unfortunately, elimination of host fish, destruction of habitats due to sedimentation, impoundment of streams

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and rivers, release of environmental contaminants, and introduction of invasive species have reduced the number of species considered stable (Lydeard *et al*., 2004; Strayer *et al*., 2004; Bogan, 2008). In Texas, the 52 described mussel species have also been affected, with many streams and rivers unable to support mussel populations at historical levels (Howells *et al*., 1996; Howells, 2010a). As a consequence, 15 species are at present listed as state-threatened (Texas Register 35, 2010). Of the state listed species, five were added to the US Fish and Wildlife Service (USFWS) candidate species list in October 2011, whereas six others are currently being reviewed to determine whether their listing under the Endangered Species Act is warranted (Federal Register 76, 2011; Howells *et al*., 1997). As a result of these listings, mussel conservation strategies focused on protecting threatened and common species are now beginning to emerge in Texas. These strategies include demand for increased sampling efforts in river basins that have either been inadequately surveyed or require baseline survey information (Texas Wildlife Action Plan, TWAP, 2005).

The Leon River drainage, located in the Brazos River basin, has received little attention by malacologists despite historically supporting a unique freshwater mussel fauna with 16 species, including three central-west Texas endemics: *Quadrula houstonensis*, *Quadrula mitchelli*, and *Truncilla macrodon* (Table 1). Early reports for this drainage come from Singley (1893) and Strecker (1931); however, these works are dated which limits their present-day usefulness. Contemporary reports for the Leon River are based on surveys conducted within the past 20 years by private collectors and Texas Parks and Wildlife Department (TPWD) personnel (Howells, 1994, 1995, 1997, 2000, 2001, 2004, 2006). Although informative, these studies were largely opportunistic, often occurring repeatedly in the same area or in easily accessible locations. In addition, much of the survey effort expended by TPWD in the Leon River drainage was near human population centres or in nearby reservoirs (Howells, 1994, 1995, 1997, 2000, 2001, 2004, 2006). Typically, these types of habitats are not inhabited by riverine mussel species or those now listed as threatened (Howells, 2010a).

Given previous survey efforts, it can be argued that the Leon River basin has never been comprehensively surveyed for freshwater mussels. This is problematic given that federal candidate species are known to have occurred in the Leon River drainage, and their status in this drainage has not been assessed, which will probably hinder future recovery efforts for these species. Thus, the objectives of this study were to determine whether state-threatened species are still extant in

Table 1. Mussel species collected in the Leon River. Collection records are by Strecker (1931), TPWD (Howells, 1994, 1995, 1997, 2000, 2001, 2004, 2006) and the present study. Single asterisks denote species that are listed as state-threatened, and double asterisks denote species that are state-threatened and candidates for protection under the Endangered Species Act. Sculpture type denotes whether a given species is known to have some form of shell ornamentation. For example, *Q. houstonensis*, although typically unsculptured, may have faint traces of pustules mid-disk and corrugations along the posterior slope and therefore was categorized as having shell sculpture

Scientific name	Abbreviation	Sculpture type	Strecker (1931)	TPWD	Present
Amblema plicata (Say 1817)	AP	Sculptured	X	X	X
Arcidens confragosus (Say 1829)	AC	Sculptured	-	-	X
Cyrtonaias tampicoensis (Lea 1838)	CT	Unsculptured	-	X	-
Lampsilis hydiana (Lea 1838)	LH	Unsculptured	X	-	-
Lampsilis teres (Rafinesque 1820)	LT	Unsculptured	X	X	X
Leptodea fragilis (Rafinesque 1820)	LF	Unsculptured	-	X	X
Megalonaias nervosa (Rafinesque 1820)	MN	Sculptured	X	X	X
Potamilus purpuratus (Lamarck 1819)	PP	Unsculptured	X	X	X
Pyganodon grandis (Say 1829)	PG	Unsculptured	-	X	X
Quadrula apiculata (Say 1829)	QA	Sculptured	X	X	X
Quadrula houstonensis (Lea 1859)**	QH	Sculptured	X	X	X
Quadrula mitchelli (Conrad 1855)*	QM	Sculptured	X	X	-
Quadrula verrucosa (Rafinesque 1820)	QV	Sculptured	X	X	X
Truncilla macrodon (Lea 1859)**	TM	Unsculptured	X	-	-
Uniomerus tetralasmus (Say 1830)	UT	Unsculptured	-	-	X
Utterbackia imbecillis (Say 1829)	UI	Unsculptured	X	-	X

the Leon River and to assess the overall distribution and abundance of rare and common mussel species along the length of this river. In addition, shell length data were collected as a measure of the overall viability of the mussel fauna within the Leon River drainage.

METHODS

Study area

The Leon River is a major tributary of the Brazos River in the North Central Prairie and Cross Timbers regions of Central Texas (Rose and Echelle, 1981) and drains an area of 9145 km^2 upstream of Lake Belton (Rossi *et al.*, 2008). The basin has a sub-humid climate characterized by hot summers and dry winters. In general, discharge for the Leon River is low and varies considerably depending on the location within the river. For example, median discharge for the Leon River is 1.04 $m^3 s^{-1}$ near Hamilton, TX (USGS gauging station 08100000), whereas near Proctor Lake, upstream from Hamilton, median discharge is 0.10 $m^3 s^{-1}$ (USGS gauging station 08099500). Compared with other Brazos River tributaries, the Leon River is relatively large, flowing for approximately 448 km from its headwaters to its confluence with the Little River in Bell County. Three major reservoirs are located on the mainstem of the Leon River. The largest, Belton Lake, is located in Bell County, covers 50 km^2, and was completed in 1954 to control flooding within the Brazos River basin. The second reservoir, Lake Leon, is located near the headwaters of the Leon River in East Land County, was constructed to provide a reliable water supply to the upper portion of the basin, and was also completed in 1954. The third reservoir, Proctor Lake, in Comanche County, is the most recent, with construction ending in 1963, and is used for flood control and commercial and residential purposes (Harmel *et al.*, 2008).

Land use within the Leon River catchment is predominantly rangeland and agriculture (Rossi *et al.*, 2008), and both land uses have probably affected the Leon River through pesticide and fertilizer runoff and cattle encroachment. Consequently, the Leon River is currently an area of concern for impaired water quality owing to elevated bacteria levels and low dissolved oxygen (Harmel *et al.*, 2008). In general, most of the Leon River catchment is sparsely populated, with the largest population centres located downstream of Lake Belton.

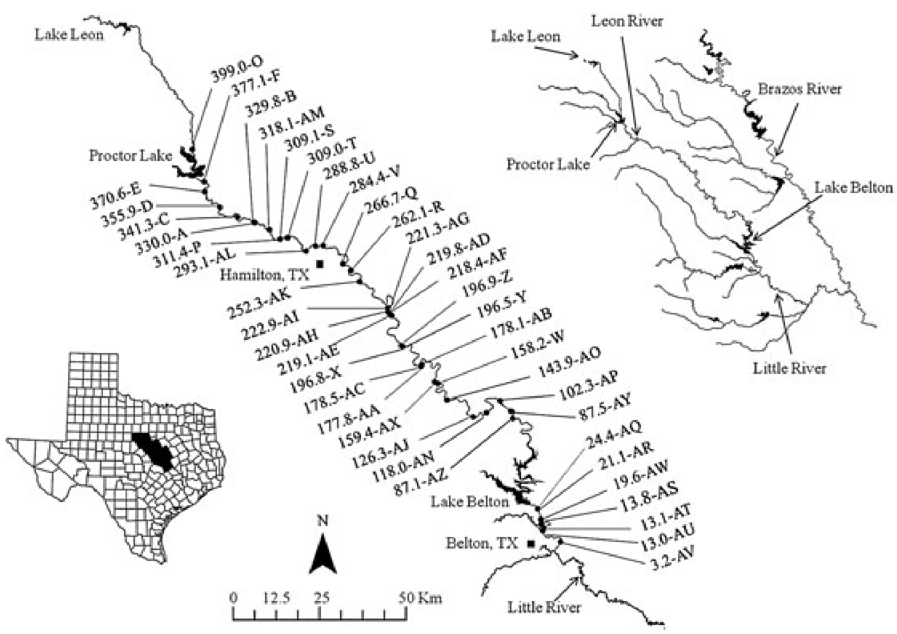

Figure 1. Map of the study area identifying the 44 sites on Leon River that were surveyed for mussels.

Table 2. Total number, univariate statistics, number of sites and catch-per-unit effort by site. *d* = Berger-Parker dominance index; *E* = Brillouin evenness index; *HB* = Brillouin diversity index; person-h = person hours sampled; and CPUE = catch-per-unit-effort (number of mussels per person-hours sampled)

LRKM	451.5-G	445.4-H	436.9-I	427.1-J	420.4-K	416.9-L	414.8-M	409.7-N	399.0-O	377.1-F	370.6-E	355.9-D	341.3-C	330.0-A
Amblema plicata	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Arcidens confragosus	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Lampsilis teres	-	-	-	-	-	-	-	-	-	26	2	4	3	4
Leptodea fragilis	-	-	-	-	-	-	-	-	-	6	3	11	11	5
Megalonaias nervosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potamilus purpuratus	-	-	-	-	-	-	-	-	-	1	-	1	-	-
Pyganodon grandis	-	-	-	-	-	-	-	-	3	5	3	-	-	-
Quadrula apiculata	-	-	-	-	-	-	-	-	-	4	-	-	-	-
Quadrula houstonensis	-	-	-	-	-	-	-	-	-	3	-	2	-	-
Quadrula verrucosa	-	-	-	-	-	-	-	-	-	17	1	5	11	-
Uniomerus tetralasmus	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Utterbackia imbecillis	-	-	-	-	-	-	-	-	1	1	-	-	-	-
Total Mussels	0	0	0	0	0	0	0	0	5	64	9	25	25	9
Total Species	0	0	0	0	0	0	0	0	3	9	4	6	3	2
d	*	*	*	*	*	*	*	*	1.67	2.46	3.00	2.27	2.27	1.80
E	*	*	*	*	*	*	*	*	0.88	0.74	0.95	0.83	0.88	1.00
HB	*	*	*	*	*	*	*	*	0.60	1.47	0.95	1.25	0.85	0.54
Person-h	*	*	*	*	*	*	*	*	2	3	3	3	2	2
CPUE	*	*	*	*	*	*	*	*	2.50	21.33	3.00	8.33	12.50	4.50

Table 2. (Continued)

LRKM	329.8-B	318.1-AM	311.4-P	309.1-S	309.0-T	293.1-AL	288.8-U	284.4-V	266.7-Q	262.1-R	252.5-AK	222.9-AI	221.3-AG
Amblema plicata	-	-	-	-	-	-	-	-	1	-	1	71	51
Arcidens confragosus	-	-	-	-	-	-	-	-	-	-	-	1	-
Lampsilis teres	3	12	4	1	1	-	2	1	13	4	5	7	3
Leptodea fragilis	7	10	7	-	6	9	7	5	-	1	16	18	10
Megalonaias nervosa	-	-	-	-	-	-	-	-	-	-	-	8	2
Potamilus purpuratus	-	-	-	-	1	-	-	-	-	-	-	2	1
Pyganodon grandis	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula apiculata	-	-	-	-	-	-	-	-	-	-	-	2	6
Quadrula houstonensis	-	1	-	1	-	-	-	-	-	-	-	49	93
Quadrula verrucosa	5	2	-	85	27	2	2	6	1	1	8	99	12
Uniomerus tetralasmus	-	-	-	-	-	-	-	-	-	-	-	-	-
Utterbackia imbecillis	-	-	1	-	-	-	-	-	-	3	-	-	-
Total Mussels	15	25	12	87	35	11	11	12	15	9	30	257	178
Total Species	3	4	3	3	4	2	3	3	3	4	4	9	8
d	2.14	2.08	1.71	1.02	1.30	1.22	1.57	2.00	1.15	2.25	1.88	2.60	1.91
E	0.95	0.75	0.79	0.10	0.49	0.65	0.81	0.82	0.40	0.88	0.79	0.69	0.62
HB	0.85	0.89	0.69	0.10	0.60	0.36	0.69	0.72	0.36	0.87	0.95	1.47	1.23
Person-h	3	3	4	3	3	2	2	2	2	2	2	4	3
CPUE	5.00	8.33	3.00	29.00	11.67	5.50	5.50	6.00	7.50	4.50	15.00	64.25	59.33

Table 2. (Continued)

LRKM	220.9-AH	219.8-AD	219.1-AE	218.4-AF	196.9-Z	196.8-X	196.5-Y	178.5-AC	178.1-AB	177.8-AA	159.4-AX	158.2-W	143.9-AO
Amblema plicata	14	80	72	52	-	2	2	5	-	1	-	1	-
Arcidens confragosus	-	-	-	1	-	-	-	-	-	-	-	-	-
Lampsilis teres	3	8	-	1	-	-	-	-	-	1	1	-	5
Leptodea fragilis	2	12	4	4	5	-	1	-	3	4	13	4	2
Megalonaias nervosa	-	12	3	7	20	12	7	1	-	-	2	2	4
Potamilus purpuratus	-	-	-	-	-	-	-	1	-	-	-	-	-
Pyganodon grandis	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula apiculata	1	1	6	11	-	-	-	-	-	-	-	-	-
Quadrula houstonensis	28	86	90	158	2	14	23	3	7	9	17	3	7
Quadrula verrucosa	8	61	30	55	23	14	7	4	-	5	18	3	27
Uniomerus tetralasmus	-	-	-	-	-	-	-	-	-	-	-	-	-
Utterbackia imbecillis	-	-	-	-	-	-	-	-	-	-	-	-	-
Total Mussels	56	260	205	289	50	42	40	14	10	20	51	13	45
Total Species	6	7	6	8	4	4	5	5	2	5	5	5	5
d	2.00	3.02	2.28	1.83	2.17	3.00	1.74	2.80	1.43	2.22	2.83	3.25	1.67
E	0.73	0.76	0.69	0.61	0.77	0.89	0.72	0.89	0.87	0.82	0.80	0.96	0.73
HB	1.18	1.43	1.20	1.22	0.98	1.11	1.02	1.10	0.48	1.08	1.16	1.16	1.05
Person-h	2	3	3	5	3	2	2	2	4	4	26	3	3
CPUE	28.00	86.67	68.33	57.80	16.67	21.00	20.00	7.00	2.50	5.00	1.96	4.33	15.00

Table 2. (Continued)

LRKM	126.3-AJ	118.0-AN	102.3-AP	87.5-AY	87.1-AZ	24.4-AQ	21.1-AR	19.6-AW	13.8-AS	13.1-AT	13.0-AU	3.2-AV
Amblema plicata	-	-	3	-	-	-	-	8	-	-	-	-
Arcidens confragosus	-	-	-	-	-	-	-	-	-	-	-	-
Lampsilis teres	-	-	1	-	-	-	-	-	-	-	-	-
Leptodea fragilis	-	2	-	4	39	-	-	-	-	-	-	-
Megalonaias nervosa	-	1	8	-	-	-	-	-	-	-	-	-
Potamilus purpuratus	-	-	-	-	-	-	-	-	-	-	-	-
Pyganodon grandis	-	-	-	-	-	1	8	-	-	-	-	-
Quadrula apiculata	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula houstonensis	4	20	-	-	11	-	-	4	-	-	-	-
Quadrula verrucosa	11	12	5	-	1	-	-	-	-	-	-	-
Uniomerus tetralasmus	-	-	-	-	-	-	-	-	-	-	-	-
Utterbackia imbecillis	-	-	-	-	-	-	-	-	-	-	-	-
Total Mussels	15	35	17	4	51	1	8	12	0	0	0	0
Total Species	2	4	4	1	3	1	1	2	0	0	0	0
d	1.36	1.75	2.12	1.00	1.31	1.00	1.00	1.50	*	*	*	*
E	0.82	0.68	0.85	N/A	0.54	N/A	N/A	0.91	*	*	*	*
HB	0.48	0.83	0.96	0.00	0.55	0.00	0.00	0.52	*	*	*	*
Person-h	2	3	2	2	15	2	2	19	1	1	1	1
CPUE	7.50	11.67	8.50	2.00	3.40	0.50	4.00	0.63	*	*	*	*

Site selection

The following criteria were used to select sites for sampling the mainstem of the Leon River: (1) had public access; (2) not located within a reservoir; (3) contained suitable mussel habitat; and (4) mussels were present during a cursory visual or tactile survey. Suitable mussel habitat was defined as a riffle or run habitat with a stable mixture of sand, gravel, or cobble substrates. Fifty-two potential sites were selected for sampling; eight of these located upstream of Leon River km (LRKM) 409 were not sampled because they had gone dry before the survey. The remaining 44 sites, located along a 396 km stretch of the Leon River, were qualitatively sampled for mussels between May and August 2011 (Figure 1). Sites ranged from 35 to 405 m in length and 1.5 to 41.1 m in width. No effort was made to sample reservoirs in the catchment as these are not likely to be inhabited by state-threatened mussel species.

Survey methodology

Surveys were conducted following Metcalfe-Smith *et al.* (2000) with surveyors qualitatively searching for mussels for a minimum of 1 person-hour (p-h) at each site. If live or fresh-dead mussels were collected during that effort, surveyors searched for a second p-h. Additional search periods were added until no new species were collected, and the total search effort exerted at each site was then recorded. Surveyors at each site used a combination of visual and tactile search methods that included observers using their hands to rake through the substrate, brush away sediment, and flip over non-embedded rocks. Effort was made to examine all available habitats during each sampling period.

All live mussels were kept in mesh bags and submersed in water until the site survey was complete. Following completion of the survey, mussels were identified to species using standard taxonomic references (Howells *et al.*, 1996; Howells, 2010b) and then returned to their approximate collection locations. Shell length (SL; anterior to posterior margins) was measured with calipers to the nearest 0.1 mm and included individuals categorized as very recently dead. Data from the timed searches were analysed to provide a total species list for each site, species richness by site (number of species observed), total abundance by site (number of individuals observed per timed search), and catch per unit effort (CPUE; number of mussels per person-hour (/p-h)). Field surveys were conducted during low flow conditions to maximize sampling effectiveness.

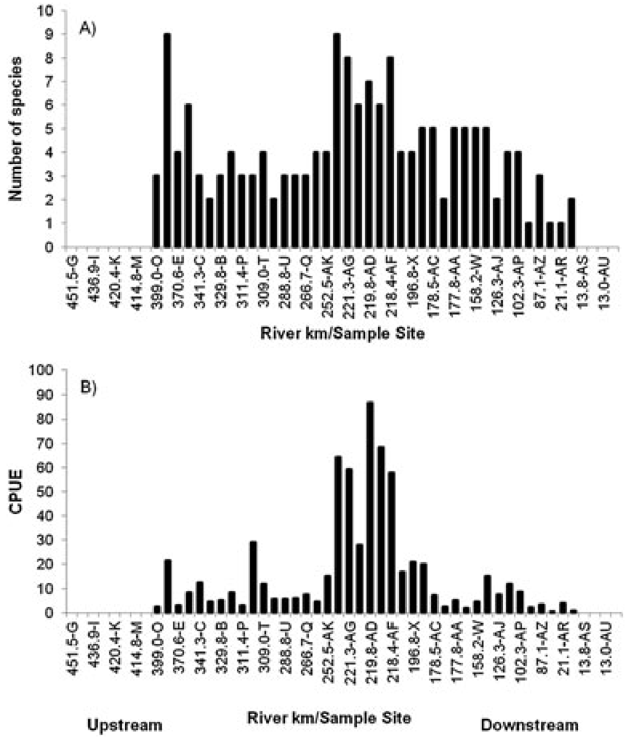

Figure 2. (A) Species richness and (B) catch per unit effort of mussels at the 44 sample sites.

Length–frequency histograms using 5 mm bins were created for the two most abundant lentic (i.e. standing water) species (*Leptodea fragilis* and *Lampsilis teres*) and lotic (i.e. flowing water) species (*Q. houstonensis* and *Q. verrucosa*) collected during this study. These histograms were used to identify individual recruitment cohorts and to assess qualitatively the viability of these species throughout the river. Individuals < 40 mm in length were considered recent recruits (Obermeyer, 1998; Ahlstedt *et al.*, 2005; Mohler *et al.*, 2006; Chapman and Smith, 2008). The median shell lengths of these species were plotted against LRKM to evaluate the spatial variability in recruitment. These four species were selected because they vary in their response to environmental extremes and are widely distributed throughout the Leon River. *Leptodea fragilis* and *L.*

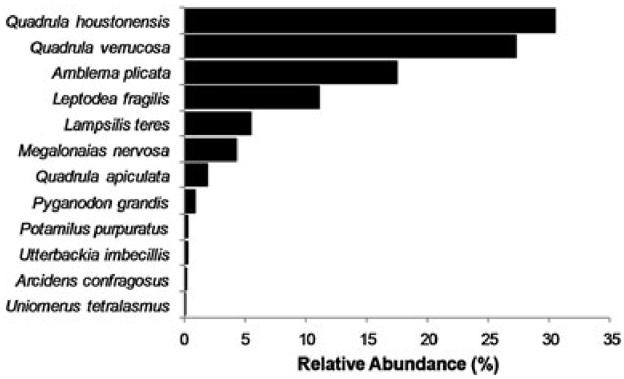

Figure 3. Relative abundance of mussel species in the Leon River.

teres are habitat generalists and relatively tolerant of environmental perturbations (Randklev *et al.*, 2011), whereas *Q. houstonensis* and *Q. verrucosa* are lotic species and, as such, are less tolerant of environmental perturbations (Howells *et al.*, 1996; Howells, 2010a).

Statistical analysis

Data from all sites were analysed using the R statistical package (R Development Core Team, http://www.R-project.org) to determine the Berger–Parker dominance index (*d*), Brillouin evenness index (*E*), and Brillouin diversity index (*HB*) calculated on a $\log_e$ scale. Non-metric multidimensional scaling (NMDS) overlain with polygons constructed from agglomerative cluster analysis was used to visually compare overall differences in mussel community structure between collection sites. NMDS maps were used to show community dissimilarities in ordination space. The degree to which the biplot accurately represents actual dissimilarities is measured by comparing the rank order of the ordination distances and dissimilarities, and the resulting value is termed stress (*S*). Typically, stress values < 0.2 indicate a good match between ordination distances and observed dissimilarities (Quinn and Keough, 2002). In addition to stress, overlaying the results of the cluster analysis in the biplot provides an additional cross-check to validate NMDS groupings. For this study, similarity was measured using the Morisita–Horn index, and cluster analysis was performed using average linkage.

Whittaker's measure (β_W) and Watters (1994) description of shell sculpture and shape were used to evaluate species turnover and the change in the ratio of sculptured to unsculptured species between Proctor Lake and Lake Belton, respectively. β_W uses presence/absence data to measure the change (i.e. turnover) in species composition between adjacent sample sites along an environmental gradient. Paired sites that lose or gain species will have higher β_W values than sites where community composition remains relatively unchanged (Magurran, 1988). With regard to shell ornamentation, shell sculpturing may help individuals stay anchored within the stream bottom, whereas individuals with unsculptured

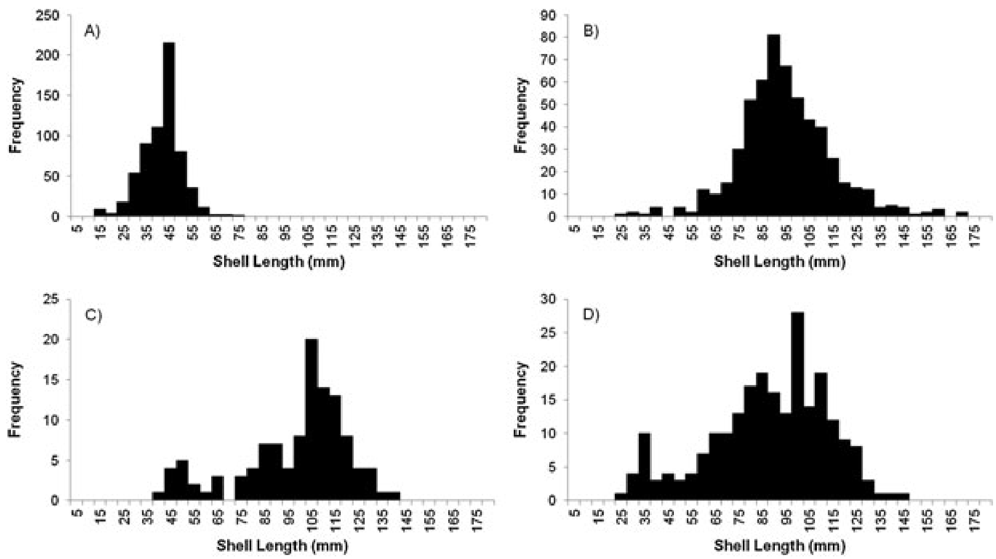

Figure 4. Size frequency distributions (shell length, mm) of (A) *Quadrula houstonensis*, (B) *Quadrula verrucosa*, (C) *Lampsilis teres*, and (D) *Leptodea fragilis*.

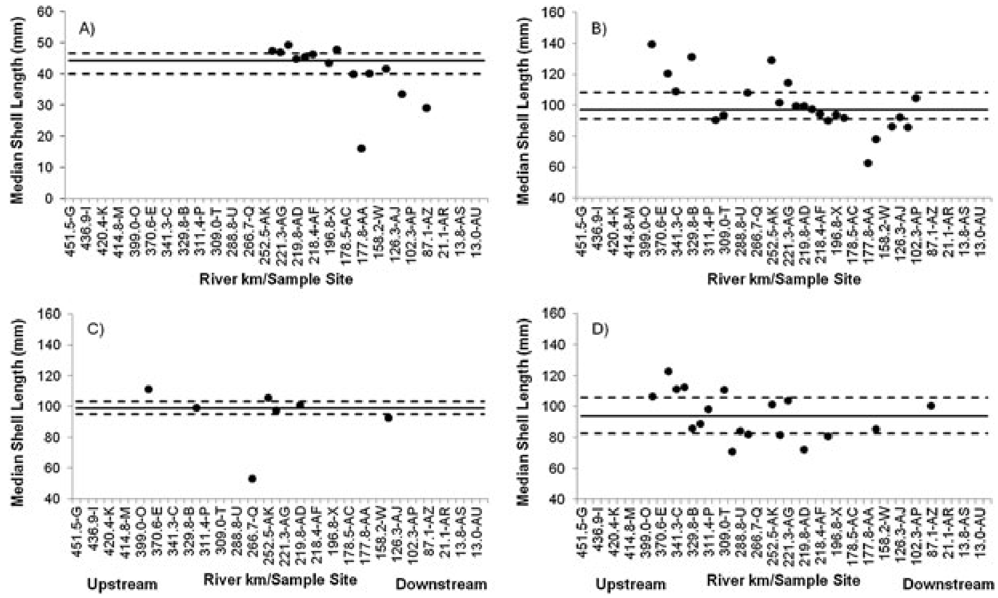

Figure 5. Median shell lengths (mm) for four mussel species collected during this study: (A) *Quadrula houstonensis*, (B) *Quadrula verrucosa*, (C) *Lampsilis teres*, and (D) *Leptodea fragilis*. Lengths are shown only for sites where five or more individuals were collected. Lines indicate overall values of the median (solid) and 25th and 75th percentiles (dashed).

shells are thought to be able to re-burrow more rapidly following dislodgement (Watters, 1994; Hornbach *et al*., 2010). Thus, these generalized forms represent two different adaptive strategies to disruptive flow, with unsculptured species being more tolerant of hydrologic variability (Watters, 1994).

RESULTS

In total, 2081 live mussels representing 12 species were collected from the mainstem of the Leon River, including the federal candidate species, *Q. houstonensis* (Table 2). Generally, mussels were distributed between Proctor Lake and Lake Belton. Mussels were collected at one locality upstream of Proctor Lake (LRKM 399.0-O) and at three localities (LRKMs 24.4-AQ, 21.1-AR, and 19.6-AW) downstream of Lake Belton. Mussel community composition at those localities comprised species that are tolerant of stressful environmental conditions. The exception was LRKM19.6-AW, where both *Amblema plicata* and *Q. houstonensis* were collected; however, no evidence of recruitment was found at this site. Overall, sample sites in the middle portion of the study area (LRKMs 222.9–218.4) were species-rich, whereas those near Proctor Lake and Lake Belton were largely depauperate (Figure 2). Site 377.1-F was the exception as it contained a mix of lotic and lentic mussel species, probably because of its close proximity to Proctor Lake. *Quadrula houstonensis*, the only state-threatened species collected during the survey, was predominantly found between LRKMs 222.9 and 87.1, but a few scattered individuals (< 3 mussels per site) were collected between LRKMs 377.1 and 309.1.

Species richness ranged from 0 to 9 species collected at each site ($x \pm SE$; 3.75 ± 0.35) and was highest between LRKMs 222.9 and 218.4, where richness ranged between 6 and 9 species (Table 2, Figure 2(a)). For sites near Proctor Lake and Lake Belton, species richness was generally low and increased with distance from the impoundments (Figures 1 and 2(a)). The number of live mussels collected at a site was variable, ranging from 0 to 289 individuals (48.3 ± 11.3). *Quadrula houstonensis* was the most abundant species, found at 23 sites and accounting for 31% of all mussels recorded in the timed searches. *Quadrula verrucosa* was the most widely distributed species, occurring at 32 of the 44 survey locations, and was the second most abundant, accounting for 27% of all mussels collected (Figure 3). *Amblema plicata* and *L. fragilis* were the third and fourth most abundant

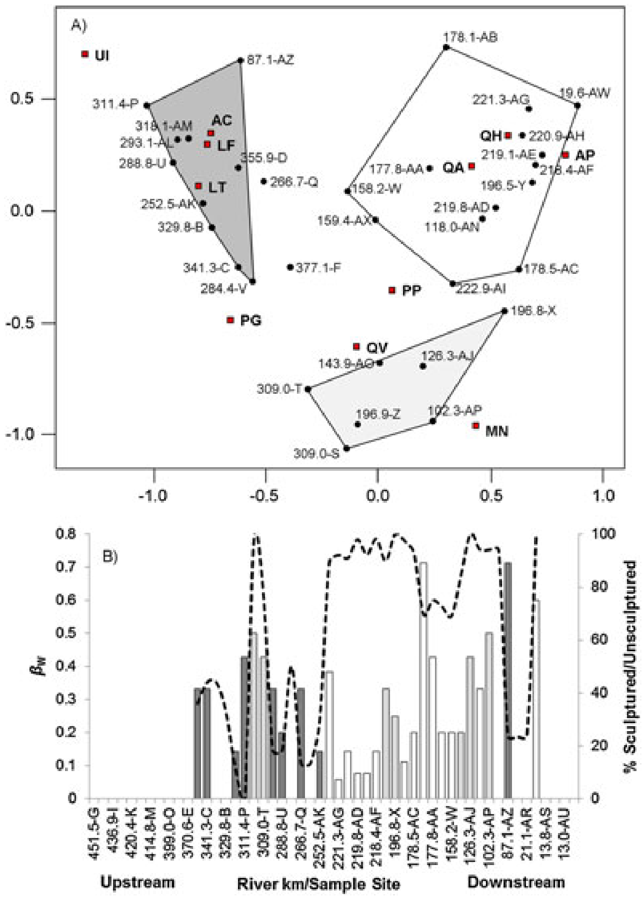

Figure 6. (A) NMDS biplot of mussel community composition ($S = 0.065$) in the Leon River. Species abbreviations are listed in Table 1. Sites with less than 10 individuals were omitted from the analyses, and shaded polygons correspond to the following communities: lentic (dark grey), lotic (white), and transitional (light grey). (B) Whittaker's measure (β_W) of species turnover by faunal grouping (dark grey = lentic, white = lotic, and transitional = light grey) overlain with the percentage of sculptured to unsculptured mussel species (dashed); the sculpture types are listed in Table 1.

species and accounted for 18% (16 sites) and 11% (30 sites) of all mussels recovered, respectively (Figure 3). *Amblema plicata* occurred at 16 sites, mostly near Hamilton, TX, whereas *L. fragilis* ranged throughout much of the Leon River, occurring at 30 of the 44 sampling localities. No other species accounted for more than 10% of all mussels collected during the survey (Figure 3). CPUE ranged from 0.00 to 89.67 mussels/p-h (14.82 ± 3.15) and was highest at LRKM 219.8, with a CPUE of 89.67 mussels/p-h. Overall, mussel abundance was highest between LRKMs 222.9 and 218.4, where CPUE ranged from 57.80 to 89.67 mussels/p-h (Figure 2(b)).

Recruitment

Recent recruitment, represented by individuals lessthan 40 mm, was observed for seven species: *A. plicata*, *L. teres*, *L. fragilis*, *P. grandis*, *Q. apiculata*, *Q. houstonensis*, and *Q. verrucosa*. No recent recruits were collected for *A. confragosus*, *M. nervosa*, *P. purpuratus*, or *U. imbecillis*. *Quadrula houstonensis* had the highest percentage of the population (27%) represented by recent recruits. *Pyganodon grandis* (10%) and *L. fragilis* (9%) had the second and third highest percentages, respectively, of recent recruits within the population. The small sample size of *P. grandis* (N = 20) makes it difficult to determine whether this percentage is an accurate representation of the age-class structure of the populations or is merely the result of sampling bias. No other species had a population comprising more than 2% recent recruits.

Quadrula houstonensis and *Q. verrucosa* exhibited unimodal length–frequency distributions (Figure 4(a), (b)). Owing to variations in individual growth rates, individual age cohorts could not be discerned from the modal peaks for these species. *Lampsilis teres* exhibited two distinct modal peaks, one from 30 to 70 mm and the other from 100 to 125 mm (Figure 4(c)). The cohort between 30 and 70 mm represents recruitment that had probably occurredwithin the last 3 years (Haag and Rypel, 2011). *Leptodea fragilis* had a trimodal distribution and exhibited distinct cohorts between 25 and 50 mm, 75 and 100 mm, and 100 and 125 mm (Figure 4(d)). As with *L. teres*, individuals in the smallest size cohort, 25 to 50 mm, are probably recruits from the past 3 years. Although no distinct recruitment cohorts are apparent within the length–frequency histograms for *Q. houstonensis* and *Q. verrucosa*, the presence of smaller individuals indicates that these species are recruiting within the river.

The median lengths of *Q. verrucosa* and *L. fragilis* were higher at sites immediately downstream from Proctor Lake and then decreased with distance from the reservoir (Figure 5(b), (d)). For *Q. houstonensis*, median length decreased downstream from Hamilton, TX, with sites in the lower portion of the Leon River being largely composed of juveniles (Figure 5(a)). The median length for *L. teres* remained largely constant, irrespective of stream position (Figure 5(c)). The overall pattern in median shell length demonstrates that recruitment is occurring in the lower portions of the Leon River and generally absent, or at least infrequent, in stream segments near Proctor Lake.

Community composition

Mussel community composition within the Leon River appeared to be fragmented with three distinct mussel communities (Figure 6(a)). In stream segments near Proctor Lake and Lake Belton (LRKMs 355-266 and 87) community composition was generally dominated by unsculptured species, such as *L. fragilis* and *L. teres*, which tend to be more tolerant of environmental disturbance (Figure 6(a), dark grey polygon). Species turnover was also high, indicating that within these stream segments, species are frequently lost or gained between paired sample sites (Figure 6(b), dark grey bars). Just downstream of Hamilton, TX (LRKMs 223-158), sculptured species, including *A. plicata*, *Q. apiculata*, *Q. houstonensis*, and *Q. verrucosa*, characterized the mussel fauna in these stream segments (Figure 6(a), white polygon). While *A. plicata* and *Q. apiculata* are generalists, *Q. houstonensis* and *Q. verrucosa* are considered generally intolerant of environmental perturbations and were the dominant species within this faunal grouping. As a corollary, species turnover was relatively low with the exceptions of Site 222.9-AI, where the mussel community changed from lentic to lotic, 178.1-AB and 177.8-AA, and where unsculptured species were proportionately more abundant compared with other sites within this grouping (Figure 6(b); white bars). Although more difficult to interpret, the final grouping within the mainstem of the Leon River included sites that appeared to represent stream segments where dominance shifts among sculptured species (Sites 196.9-Z and 196.8-X) or there were sizeable shifts in the percentage of sculptured to unsculptured species (309.1-S, 309.0-T, 143.9-AO, 126.3-AJ, and 102.3-AP) (Figure 6(a), light grey polygon). As a result, these sites were characterized by relatively high species turnover (Figure 6(b), light grey bars).

DISCUSSION

Historical and recent mussel surveys have recorded 16 mussel species from the mainstem of the Leon River. This study documented the presence of 12 live mussel species, including one federal candidate species (*Quadrula houstonensis*) and two new records (*Arcidens confragosus* and *Uniomerus tetralasmus*). The mussel fauna of this river is dominated by *Q. houstonensis*, *Q. verrucosa*, *A. plicata* and *L. fragilis*, which is comparable with other studies from this river (Table 1). However, no live individuals or shell material for three species known to have historically occurred in the Leon River were found. The last collections of *L. hydiana*, *Q. mitchelli* and *T. macrodon* in the mainstem of the Leon River are those by J. K. Strecker (1931) in the early 1930s. Museum records suggest that all three of these species were abundant at the sites where they were collected (C.R. Randklev, unpublished data). *Lampsilis hydiana* was collected during surveys of Lake Belton (Howells, 1997), and fresh-dead individuals of *Q. mitchelli* were encountered near Belton, TX by an amateur malacologist during the early 1990s (R. G. Howells, personnel communication, 2011). Despite surveying reaches upstream and downstream of Lake Belton and Proctor Lake, no live individuals or shell material were found for either species. Because *L. hydiana* and *Q. mitchelli* were recorded sparingly in contemporary surveys and were not found during this study, both are probably locally extinct or extremely rare in this basin. For *T. macrodon*, more than 80 years have passed since live individuals or shell material has been collected in the Leon River. However, in 2009, live individuals for this species were collected in the Little River, which is formed by the confluence of the Leon and Lampasas Rivers, upstream from the Brazos River (Jack Davis, personnel communication). Based on this finding and the results of the present survey, if this species does occur in the Leon River, it is likely to be in stream segments that are directly connected to the Little River.

Despite not being reported historically, fresh-dead individuals of *Cyrtonaias tampicoensis* have been collected from the middle and lower portions of the Leon River, including Lake Belton (Howells, 1997, 2001; R. G. Howells, personnel communication). In addition, live individuals for this species were recently collected in the Little River, just upstream from the mainstem of the Brazos River (Karatayev and Burlakova, 2008). During the survey, no live individuals of this species were encountered, but subfossil shell material was collected at several sites downstream of Lake Belton. Thus, *C. tampicoensis* seems to occur in the Leon River but is uncommon to rare and appears to be restricted to the lower portions of the river.

Two species (*Arcidens confragosus* and *Uniomerus tetralasmus*) that were not previously reported were collected and thus are new records for the Leon River. *Arcidens confragosus* is rare to uncommon throughout its range (Howells *et al*., 1996) and typically does not reach high densities at localities where it is present. Hence, this species was probably overlooked during previous surveys. *Uniomerus tetralasmus* is tolerant of a variety of environmental conditions, including habitats that are prone to frequent drying (Byrne and McMahon, 1994), and can reach high densities in habitats unsuitable for other mussel species (Howells *et al*., 1996). Although *U. tetralasmus* has been documented surviving emersion for extended periods of time (Byrne and McMahon, 1994) and could theoretically persist in the dry, upstream portions of the river, it is unlikely that it inhabits this reach in high densities given high summer temperatures in central Texas combined with drought conditions in recent years. Since this species was only encountered at one sample site, it is most likely rare to uncommon or restricted to sites within the Leon River where mussel habitat has been heavily degraded.

The presence of a wide range of size classes for multiple species indicates that the Leon River is still capable of supporting a mussel fauna. Typically, older, larger individuals dominate mussel populations that have been affected by human activities because recruitment has ceased (Layzer *et al*., 1993; Heinricher and Layzer, 1999; McMurray *et al*., 1999; Vaughn and Spooner, 2004; Moles and Layzer, 2008). Therefore, the presence of multiple size classes demonstrates that reproduction has not ceased in the river and that some species are recruiting juveniles. More specifically, the presence of smaller *Q. houstonensis* is particularly encouraging because of the increasing rarity of this species within Texas (Howells, 2010a; Texas Register 35, 2010; Federal Register 76, 2011). Although recruits were observed for *Q. verrucosa*, the low percentage of mussels less than 40 mm that were collected is troubling for the long-term survival of this population.

Although recruitment was evident, there were several indicators that human actions had affected reproduction within the river. First, the low abundances and lack of smaller individuals of some long-lived lotic species, including *A. confragosus*, *M. nervosa*, and *Q. apiculata*, indicated that these species are not actively recruiting within the river and may be at risk of extirpation in the future. Second, the absence of smaller individuals of long-lived species (e.g. *Quadrula* spp.) at sites closest to Proctor Lake indicated that habitat in these reaches is largely unsuitable for supporting mussel reproduction for species that are known to have occurred historically in this basin. This point was further supported by the presence of and, in some cases, the high abundance of opportunistic mussel species (e.g. *Lampsilis teres*, *Pyganodon grandis*, and *Leptodea fragilis*) in these reaches. Third, in the downstream portions of the Leon River (LRKMs 196.5-87.1), populations of long-lived species were either dominated by smaller size classes, as in *Q. houstonensis* for which 51% of the individuals collected were less than 40 mm in SL, or reveal little to no evidence of recent recruitment (e.g. *Quadrula verrucosa*, *Amblema plicata* and *Megalonaias nervosa*). These patterns by themselves are not problematic as they might reflect reproductive heterogeneity stemming from natural environmental variability, but combined with declines in species richness, abundance, and high species turnover, suggest that conditions are deteriorating within the Leon River.

Hydrologic variability, particularly the frequency and magnitude of droughts and spates, can affect the distribution of freshwater mussels (Strayer, 1993; Di Maio and Corkum, 1995). Mussels exposed to low-flow conditions are subjected to reduced oxygen concentrations, increased water temperature, and shrinking habitat, whereas at high flows, increased velocity and hydraulic forces on the stream bed can be equally detrimental

(Strayer, 1999; Johnson, 2001; Golladay *et al*., 2004; Morales *et al*., 2006; Gangloff and Feminella, 2007; Brainwood *et al*., 2008; Haag and Warren, 2008; Zigler *et al*., 2008). During the survey, flow between Proctor Lake and Lake Belton was at or below the 25th percentile of base flow, above Proctor Lake the river was dry except for a few isolated stagnant pools, and downstream from Lake Belton flow was largely stagnant. Although the response of mussels to these changing habitat conditions was not measured, mortality for lotic species appeared highest in those reaches where channel shrinkage was severe or the river was reduced to stagnant, isolated pools. These areas occurred primarily between LRKMs 377-252 and 196-87, and they coincided with low species richness and CPUE (Figure 2). These observations, in conjunction with the fact that the survey occurred during the worst drought on record in Texas indicates that summer-time flow releases from nearby reservoirs, especially during periods of low precipitation or extreme drought, are largely inadequate to sustain existing mussel populations.

The construction of multiple reservoirs along the entire length of the Leon River has undoubtedly influenced freshwater mussel assemblages in this basin. Dams fundamentally transform river ecosystems by altering hydrologic regimes, eliminating and/or fragmenting habitats, and disrupting patterns of energy flow (Poff *et al*., 1997, Rosenberg *et al*, 2000; Pringle, 2003; Graf, 2006; Hoeinghaus *et al*., 2009; 2007;). The ecological ramifications of these alterations vary at multiple spatio-temporal scales but often lead to reductions in mussel abundance and the extirpation of rare species (Vaughn and Taylor, 1999; Haag and Warren, 2010). In the Leon River, mussel species richness and abundance increased with distance downstream from Proctor Lake and peaked at mid-reaches near Hamilton, TX (Figure 2(a) and 2(b)). Changes in community composition followed a similar pattern, with sites near Proctor Lake and Lake Belton having high species turnover and being generally dominated by unsculptured lentic species (Figure 6(b)). Median shell length for lotic species followed a similar pattern, with younger individuals becoming more abundant with distance from the reservoir (Figure 5). Above Proctor Lake, the absence of mussels was most likely the result of inadequate instream flows and the dam itself. The physical presence of an impoundment impedes the upstream migration of fish bearing glochidia (juvenile mussels) (Watters, 1996). Thus, if mussels were present following the construction of Proctor Lake, stochastic events (e.g. drought) combined with suppressed recruitment from downstream populations could have conceivably eliminated these isolated mussel communities.

In general, this study's observations mirror those from similar studies performed downstream from impoundments (Vaughn and Taylor, 1999; Hornbach *et al*., 2010). However, subsequent declines in reaches downstream of Hamilton, TX, near LRKM 218.4 (Figure 2) do not meet empirical expectations regarding mussel recovery downstream from reservoirs. High species turnover and shifts in community composition downstream of LRKM 178.5 underscore this point (Figures 5 and 6). Thus, these observations are unexpected and suggest that more localized disturbances stemming from poor land management practices and the lack of groundwater input to offset low instream flows may be having a greater impact than impoundments on mussel populations in these reaches.

The conversion of natural landscapes to agriculture or urban centres introduces a variety of stresses to a river ecosystem that can directly or indirectly damage unionid mussels by eliminating habitat or fish hosts required to reproduce (Brim Box and Mossa, 1999; Poole and Downing, 2004; Lyons *et al*., 2007). Although studies identifying specific linkages between agricultural land use and mussel declines are lacking (Newton *et al*., 2008), mussels and their host fish are probably affected by higher inputs of sediments, nutrients, and pesticides that accompany agricultural landscapes (see Allan, 2004 for a general review). These impacts can alter levels of primary production, which can inhibit growth and reproductive output of mussel communities (Haag and Rypel, 2011). Riparian deforestation is also a concern because it can exacerbate inputs of organic and inorganic pollutants and destabilize stream banks, leading to highly entrenched streams that experience severe bed scouring during high flows (Naiman and Decamps, 1997; Brim Box and Mossa, 1999; Poole and Downing, 2004). For the Leon River, riparian deforestation was especially apparent at sample sites (LRKMs 178-102) downstream from Hamilton, TX, which seems to coincide with this study's observations of low mussel abundance and species richness in these stream segments. In addition, the mussel fauna at these localities is largely comprised of lentic species or those with unsculptured shell morphology. At these sites, the stream banks were often heavily incised, and a fine layer of silt was present throughout most habitat types. While these observations are largely anecdotal, they do suggest that mussel habitat is or has been degraded by nearby agricultural practices.

Cattle encroachment, although less studied, is also detrimental to mussel populations through trampling, increased sedimentation, and nutrient inputs (Brim Box and Mossa, 1999). Although the impact of livestock on water quality in the Leon River has not been well examined, studies in nearby rivers with land uses similar to those of the Leon River basin have documented degraded water quality stemming from the presence of dairy farms and agriculture (Rossi *et al*., 2008). During the study, cattle were observed throughout the study area but were most noticeable in the reaches at or downstream of Hamilton, TX. In areas routinely used by livestock, water quality was noticeably degraded; in some stream segments, water colour changed from light brown to black, macrophytes became more prevalent, and the substratum was covered with filamentous algae. These observations suggest that farming and livestock are reducing water quality in portions of the Leon River. However, the relative importance of these impacts on observed mussel declines and how these impacts are influenced by inadequate instream flows and nearby reservoirs remain unknown.

Despite the historic impacts of impoundments and surrounding land use on the native mussel fauna, downstream populations could be restored through thoughtful management practices. The Reservoir Release Improvement (RRI) programme has been cited as the putative factor responsible for the recovery of several federally endangered mussel species in the Duck River, Tennessee (Hubbs *et al*., 2010). This programme was initiated in 1991 with the goal of improving minimum flows and dissolved oxygen levels downstream of the Normandy Dam, TN (Jones *et al*., 2010). Increasing abundances of freshwater mussel populations downstream of this impoundment during the past 15–20 years are believed to be the direct result of this programme, in conjunction with an effort by resource agencies and NGOs to improve water quality and riparian habitat within the catchment. The RRI could serve as an example of how managing an existing impoundment effectively could improve impaired mussel populations in this basin.

In summary, the Leon River retains a rich mussel fauna, including the presence of a candidate species for federal protection, *Q. houstonensis*. However, species richness and abundance of mussels at study sites as a whole were low, and species turnover was generally high, indicating that local and catchment-scale impacts are adversely affecting mussel populations in the Leon River. Further studies are needed, requiring not only broad-scale analyses correlating mussel declines with regional human activities but also empirical studies that evaluate the effects of specific impacts (e.g. low instream flows) on mussel populations. Studies that link both will allow conservationists and resource managers to design more effective strategies to protect the mussel fauna within and outside this basin.

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