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**Cover Photograph:** Collection of surveyed mussels. Photograph © Stephen Van Kampen Lewis.

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## Discovery of a Species Rich Assemblage of Freshwater Mussel Species in the Metropolitan Lake Houston, Harris County, Texas

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**Abstract** - Freshwater mussels are one of the most imperiled taxa globally. North American mussels have experienced rapid declines throughout the 20<sup>th</sup> and into the 21<sup>st</sup> centuries. These declines are primarily associated with habitat degradation through water quality and impacts from invasive species. In Texas, most rivers have been altered by reservoir construction, which are thought to provide suboptimal mussel habitat, including Lake Houston reservoir in Houston, Texas. We performed a 44 person-hour freshwater mussel survey to detect the presence/absence of state-listed freshwater mussels within Lake Houston, as requested by Texas Parks and Wildlife Department. We relocated 1,190 native freshwater mussels out of the project site in Lake Houston. We documented the presence of 15 mussel species within the project area, including 12 live species and recent “dead” shells of two additional species, as well as a much older shell of a 15<sup>th</sup> species. No state or federally listed species were observed. Overall, mussel density was 0.098 per square meter (980 per hectare). The total number of individuals found for each species ranged from 1 to 397, and species catch per unit effort (CPUE) ranged from 0.02 to 9.02 mussels per hour. *Cyclonaias pustulosa* and *Quadrula apiculata* were the most abundant species observed and were found at the greatest densities. The presence of *Tritogonia nobilis* was one of the most unexpected observations made. The Mussels of Texas database (MoTX) has no records of this species in the San Jacinto Basin, and the nearest observation was approximately 65 kilometers north of Lake Houston, in the Trinity River Basin. Our results suggest that, despite ecological impacts from damming and sediment deposition from frequent extreme flood events, many of the freshwater mussel species found in other portions of the San Jacinto River are persisting and could even be flourishing within Lake Houston. Our findings suggest that freshwater mussels could be a significant ecological component of the lake.

### Introduction

Freshwater mussels (order Unionida) are considered one of the most imperiled taxa in North America, experiencing rapid declines throughout the 20<sup>th</sup> and into the 21<sup>st</sup> centuries (Bogen 1993, Lydeard et al. 2004). It has been estimated that 30 freshwater mussel taxa native to North America have been pushed to extinction during the last century (Vaughn 2018). Approximately 195 species (65%) of the 300 species native to North America are currently listed as vulnerable, threatened, or endangered (Haag and Williams, 2014, Vaughn, 2017). The high degree of biodiversity loss not only impacts species richness but is also having extreme impacts on “abundant” and “common” species, resulting in substantial declines in relative abundance and biomass (Lindenmayer et al. 2011). Relative abundance and biomass have become important metrics in valuing ecosystem functionality (Gaston and Fuller 2007, Lindenmayer et al. 2011). The more abundant and the more biomass a species or species group contributes to the system, generally the more the ecosystem is reliant on that and/or those species.

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Water quality issues (i.e., pollution, temperature fluctuations), invasive species (*Dreissena polymorpha* Pallas [Zebra Mussel] and *Corbicula* sp. [Asian Clam]), river damming and reservoir creation, and the subsequent habitat alteration and degradation that result from these activities have all been identified as major factors in the decline of freshwater mussels throughout North America (Haag and Williams 2014, Vaughn and Taylor 1999, Williams et al. 1993). In East Texas, the Sabine-Trinity Province includes the Sabine, Neches, Trinity, and San Jacinto River basins. This province is considered to be the diversity hotspot for freshwater mussels within the state (Haag 2010, Burlakova et al. 2011). The San Jacinto River is located in the Sabine-Trinity Province Watershed and has undergone significant degradation in the last 90 years (Burlakova et al. 2011). In 2006, it was considered the 9<sup>th</sup> most endangered river in the United States, primarily due to sediment loading and bank erosion originating from sand mining operations (American Rivers, 2006). In addition, urban development and water diversion are identified as two major impacts to the Trinity/San Jacinto Basin (Winemiller et al. 2010). Between 2005 and 2009, 5 sites within the San Jacinto River Basin were surveyed for unionid assemblages (Burlakova et al. 2011). Evidence of only 9 extant species was found, based on live and recently-dead individuals. This led to the assumption that up to 20 of the 29 species (70%) historically found in the San Jacinto River may now be extirpated.

Lake Houston in Harris County was created 65 years ago by damming the San Jacinto River approximately 27 kilometers northeast of downtown Houston (Fig. 1). The City of Houston recently proposed a new raw water intake structure in the southern portion of Lake



Figure 1. Lake Houston in relation to Sabine-Trinity Province, as described by Haag (2010) and Burlakova et al. (2011). Inset shows survey location within the lake.

Houston. As part of the environmental permitting process, we performed a freshwater mussel survey to detect the presence/absence of state-listed freshwater mussels within or near the project area. All native freshwater mussels detected were to be collected and relocated to a nearby location within Lake Houston to protect them from potential impacts from the proposed construction.

Prior to the start of surveys, we identified 32 native mussel species with the potential to occur within or near the San Jacinto River Basin (Howells 2014), including 3 species listed by the State of Texas as threatened (*Pleurobema riddellii* Lea [Louisiana Pigtoe], *Lampsilis satura* Lea [Sandbank Pocketbook], and *Fusconaia chunii* [Lea] [Texas Pigtoe]). To the best of our knowledge, there have been 4 freshwater mussel surveys in Lake Houston prior to our study (Randklev et al. 2020). The most recent survey, in 2005, found evidence for 7 extant species in the lake, as well as evidence of 4 additional species, but these were only represented by old shells (Burlakova et al. 2011).

### Methods

We developed protocols for surveying and relocating both state-listed and common freshwater mussels, which were reviewed and approved by Texas Parks and Wildlife Department (TPWD). The designated survey area included the project footprint and a 20-meter buffer around it within 80 meters of the shoreline. The project footprint included a bridge and pier structure to support 2 concrete water pipelines extending 290 meters from the shoreline to a 70 x 37-meter water intake structure extending the project out to approximately 360 meters from shore. The entire survey area was 12,140 square meters (1.2 hectare) in size. The outermost portion of the survey area was approximately 1.1 kilometers from the original channel of the San Jacinto River (Fig. 1).

We conducted transect surveys and mussel translocations between March 25 and April 25, 2019, when water temperatures exceeded 60 degrees Fahrenheit, per TPWD protocols for aquatic relocation. Transects were laid out such that the entire survey area was surveyed, with the objective of removing all native mussels from the potential impact area. Transect ends were mapped using GPS equipment. Transects consisted of two-meter-wide corridors demarcated with weighted line. Two biologists worked side by side and conducted tactile searches for all freshwater mussels present. The first 20 transects were laid out parallel to shore. The remaining transects were laid out perpendicular to shore. In total, 44 transects were surveyed. Wading and/or snorkeling were/was used for surveys conducted in less than 1 meter of water. For surveys within depths of 1 to 2 meters, divers used a hookah system (surface pump with airlines to divers below) and in depths greater than 2 meters, SCUBA equipment was utilized. We relied entirely on tactile methods of mussel detection due to extremely low visibility of Lake Houston. During surveys, we systematically raked our fingers through all soft substrates to depths of up to 10 centimeters.

We collected all detected native mussels and placed them in mesh dive bags for the duration of the survey. At the end of each transect survey, the collected mussels were processed and identified to species. A subset of all collected mussels had their shell length measured to the nearest millimeter and photographed, including at least one representative from each native species encountered. Native mussels were kept out of the water for no more than ten minutes during processing and were stored in freshwater following processing until relocation. Mussels were typically held in captivity for two to four hours, and never longer than six hours.

The total number of mussels collected, survey duration, and number of surveyors were recorded for each transect. Catch per unit effort (CPUE) for each transect was calculated by



dividing the number of mussels captured by total person hours to determine number of mussels encountered during 1 survey hour to determine a CPUE value indicating the number of mussels encountered during 1 person-hour. CPUE was also calculated for the sections of the survey area (combining sets of transects) as well as for the entire survey area.

All collected mussels were translocated approximately 2 kilometers northeast of the survey area to a designated relocation area. Four species of native mussel were observed in the relocation area prior to transplanting mussels: *Cyclonaias pustulosa* Lea (Pimpleback), *Lampsilis teres* Rafinesque (Yellow Sandshell), *Plectomerus dombeyanus* Valenciennes (Bankclimber), and *Quadrula apiculata* Say (Southern Mapleleaf). All relocation area resident mussels appeared to be healthy and thriving, with both juvenile and adult mussels present, indicating this site was suitable for mussel relocation.

We conducted a GIS analysis using 2018 bathymetry data collected by the Texas Water Development Board (Leber et al. 2019) to calculate the amount of area within Lake Houston with the same range of depths as our survey area, assuming that substrate and habitat types remain relatively consistent throughout the lake at these depths. Using this information and the overall CPUE value we calculated for the survey area, we estimated the total number of mussels for the portion of the lake within depth range of our study.

### Results

Depths observed within the survey area ranged from 0 to 7.9 meters. This included a gradual slope of the lake bottom with water depths ranging from 0 to 2.3 meters for the first 80 meters from shore, steeper slopes with water depths ranging from 2.3 to 4.6 meters from 80 to 120 meters from shore, and a more gradual slope with water depths ranging from 4.6 to 7.9 meters from 120 to 355 meters from shore at the end of the survey area. We observed fine sand with embedded coarse gravel and flat expanses of marl (lime-rich mudstone) within the first 80 meters of the survey area, a combination of sand and silt on the steeper slope from 80 to 120 meters from shore, and mostly soft to very soft silt/clay throughout the remainder of the survey area. The range of depths at which each substrate type was observed, as well as average depth of each substrate type can be found in Table 1.

We conducted 44 person-hours of surveys and relocated 1,190 native freshwater mussels. We documented the presence of 15 mussel species within the survey area, including 12 live species and recently dead shells of two additional species, as well as a much older shell of a 15<sup>th</sup> species (Table 2). No state- or federally-listed species were observed. Overall mussel density was 0.098 per square meter (980 per hectare). The total number of individuals found

Table 1. Range of depths (in meters) at which each substrate type\* was observed, along with the average depth of each substrate type.

Substrate Type	Depth Range	Average Depth
FSaMG	0–1.37	0.76
FSaMGC	1.37–1.98	1.65
SaSiMG	1.83–2.23	2.06
SaSi	2.23–4.57	3.53
SaSiC	2.23–5.49	3.75
SiC	4.57–7.92	6.43

\*FSaMG = fine sand/marl/gravel, FSaMGC = fine sand/marl/gravel/clay, SaSiMG = sand/silt/marl/gravel, SaSi = sand/silt, SaSiC = sand/silt/clay, SiC = silt/clay.

for each species ranged from one to 397, and species CPUE ranged from 0.02 to 9.02. *C. pustulosa* and *Q. apiculata* were the most abundant species observed and were found at the greatest densities. Mussels were found in all observed substrate types, including fine soft sand, soft sand/silt, dense clay/marl with embedded coarse gravel, and very soft silt/clay. Shell length and wear data were collected for 517 individuals, representing all 12 live species observed.

CPUE for each transect ranged from 0 mussels per person-hour (first transect closest to shore) to 152 mussels per person-hour (100–165 meters from shore at depths of 2.3 to 4.6 meters), with an average CPUE of 32.8 mussels per person-hour. There appeared to be a noticeable pattern to mussel density and the frequency of detection within the survey area, with mussels being encountered at greater frequencies approximately halfway through the survey area. To illustrate this pattern, we broke the survey area into nine survey segments of approximately similar sizes based on transect configuration, and calculated CPUE values for each segment (Fig. 2).

The highest segment CPUE values were observed in segments E (64.8), F (98.8), and G (54.8) which correspond to the slope observed approximately 80 meters from shore and continuing into the flatter terrain beyond. Species richness was also calculated for each survey segment and there was a slight overall decrease in species richness as distance from shore increased (Fig. 2). Species richness ranged from 5 to 8 species per segment. The highest species richness was observed in segments A and B, the 2 segments closest to shore. Three species were found in every survey segment: Pimpleback, *Pyganodon grandis* Say (Giant Floater), and Southern Maple Leaf. Several species only occurred in the first 3 transects at depths of 0–0.6 meters, including *Lampsilis hydiana* Lea (Louisiana Fatmucket), Yellow Sandshell, *Leptodea fragilis* Rafinesque (Fragile Papershell), *Toxolasma texasiense* Lea (Texas Lilliput), and *Leaunio lienosus* Conrad (Little Spectacle Case, formerly *Villosa lienosa*). Three species only occurred in the outer 6 segments at depths of 1.4 to 7.6 meters: *Megalonaias nervosa*

Table 2. Mussel species observed in Lake Houston, Harris County, TX during 2019 survey, including total number of individuals, Catch Per Unit Effort (CPUE), density for each species, and depths. Density indicates mussels per square meter. Depths is the range of depths (in meters) each species was observed in.

Scientific Name	Common Name	# of Individuals	CPUE	Density	Depths
<i>Plectomerus dombeyannus</i>	Bank Climber	177	4.02	0.0146	0.1–6.1
<i>Potamilus purpuratus</i>	Bleufer	Shells only	N/A	N/A	N/A
<i>Truncilla truncata</i>	Deertoe	Shells only	N/A	N/A	N/A
<i>Utterbackiana suborbiculata</i>	Flat Floater	17	0.39	0.0014	1.4–7.9
<i>Leptodea fragilis</i>	Fragile Papershell	4	0.09	0.0003	0.3–1.5
<i>Pyganodon grandis</i>	Giant Floater	58	1.32	0.0048	0.1–7.9
<i>Tritogonia nobilis</i>	Gulf Mapleleaf	130	2.95	0.0107	2.3–7.9
<i>Leaunio lienosa</i>	Little Spectacle Case	1	0.02	0.0001	0.6–1.5
<i>Lampsilis hydiana</i>	Louisiana Fatmucket	3	0.07	0.0002	0.4–0.9
<i>Cyclonaias pustulosa</i>	Pimpleback	397	9.02	0.0327	0.1–7.9
<i>Quadrula apiculata</i>	Southern Mapleleaf	350	7.95	0.0288	0.1–7.9
<i>Toxolasma texasiense</i>	Texas Lilliput	3	0.07	0.0002	0.4–0.9
<i>Amblema plicata</i>	Threeridge	Shells only	N/A	N/A	N/A
<i>Megalonaias nervosa</i>	Washboard	43	0.98	0.0035	1.4–7.9
<i>Lampsilis teres</i>	Yellow Sandshell	7	0.16	0.0006	0.1–1.5

*Rafinesque* (Washboard), *Tritogonia nobilis* (Conrad) (Gulf Mapleleaf; formerly *Quadrula nobilis*), and *Utterbackiana suborbiculata* Say (Flat Floater).

CPUE may be more dependent on substrate type than depth (Fig. 3). It is also possible that depth and substrate are autocorrelated. We conducted a simple linear regression of Depth (independent variable) versus CPUE (dependent variable) resulting in a P-value of 0.06 and R<sup>2</sup> value of 0.08, indicating there is a significant correlation at the 90 percent confidence interval. In contrast, our ANOVA analysis of substrate versus CPUE provided a p-value of <0.0001. While there appears to be a slight increase in CPUE values as one moves into deeper waters, there is a much more dramatic increase once coarse gravel and marl are no longer present. CPUE then drops off somewhat when sand is no longer present. Species richness does not appear to follow this same pattern (Fig. 4). Richness remains relatively constant across the substrate types observed.

Few introduced species were encountered during surveys. We observed 17 Flat Floaters, believed to have been introduced to Texas in the mid-1900’s (Howells 2014), and approximately 12 individuals of Asian Clam. Per TPWD protocols, all invasive species found were destroyed. No evidence of Zebra Mussel was observed.

### Discussion

A search of the Mussels of Texas database (MoTX) for all species occurrences within Lake Houston, the East Fork of the San Jacinto River, the West Fork of the San Jacinto

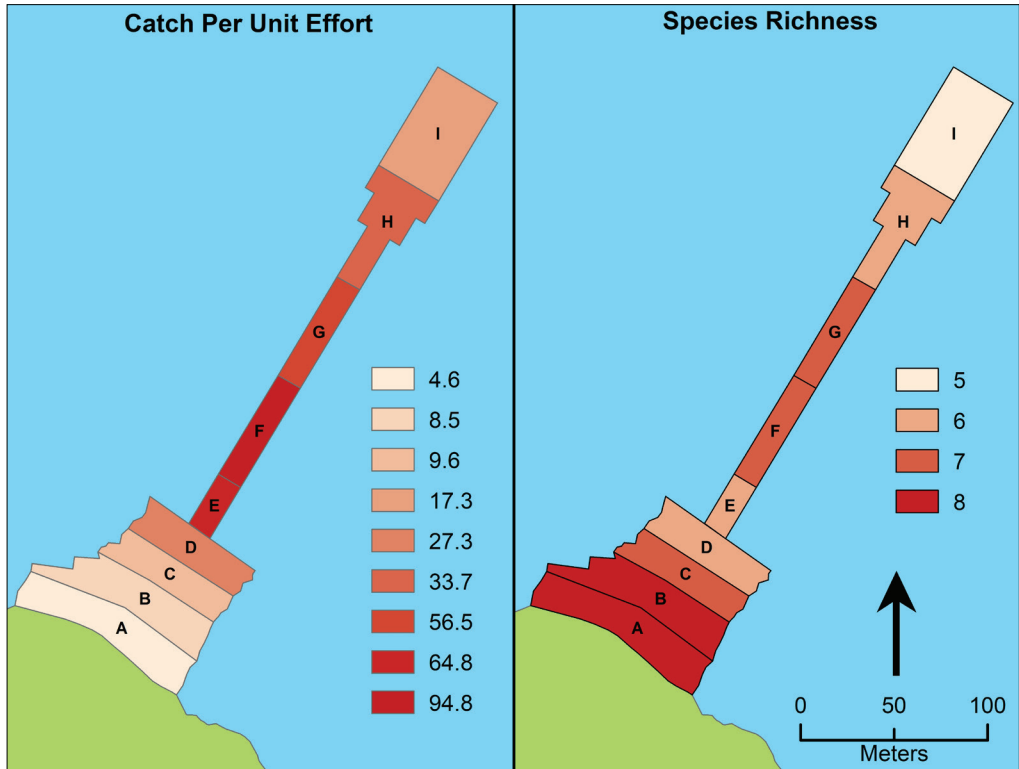


Figure 2. CPUE (mussels per hour) and Species Richness values for nine 2019 survey segments in Lake Houston. Each segment is made up of transects covering the entire segment.



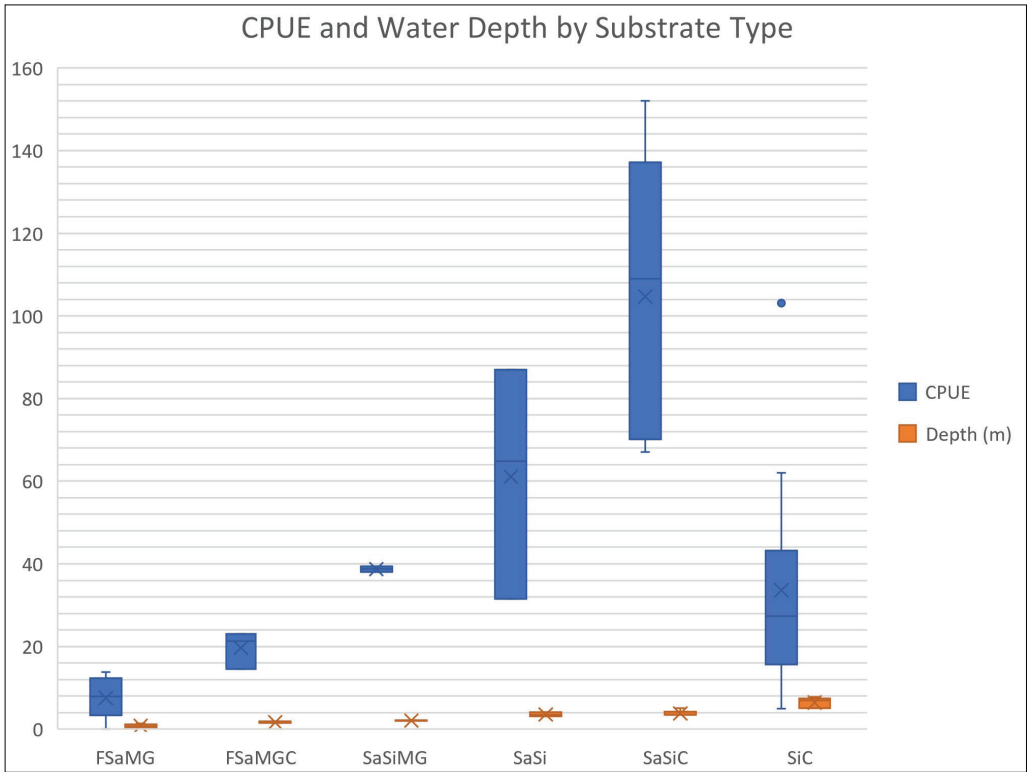


Figure 3. Averaged CPUE and Water Depth (meters) for each observed mix of substrate types.

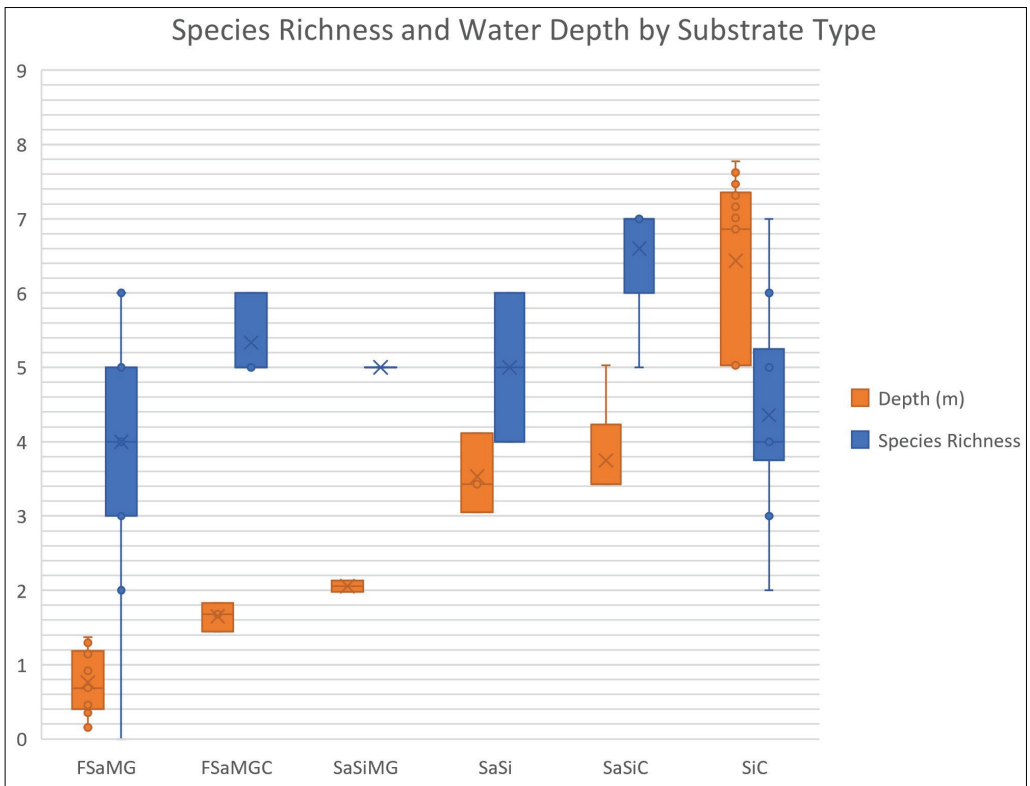


Figure 4. Averaged Species Richness and Water Depth (meters) for each observed mix of substrate types.

River, and the San Jacinto River (Randklev et al. 2020) indicated the total number of species observed within the river system was 24 (Table 3). Of these, only 16 had been observed since 2005, and only 12 species have been observed in Lake Houston (11 since 2005). In each of these surveys, some species were only represented by shells. Our research indicates there have been at least 4 surveys in Lake Houston since 1995 on the following dates: June 18, 1996; June 26, 1996; and October 7, 2005; and our survey in the spring of 2019 (Table 4). The June 18, 1996, survey appears to have occurred in the same general portion of the lake as our survey, while the other surveys occurred approximately 9.7 kilometers north (upstream) of our survey site. *Cyclonaias pustulosa* and *Q. apiculata* were the only species observed alive during all four surveys.

The most recent Lake Houston mussel survey recorded in the MoTX database occurred on October 7, 2005 (Burlakova et al. 2011). As noted earlier, this survey found evidence for 11 freshwater mussel species, but only 7 were found alive. In contrast, we observed 12 live species, and 3 additional species based on shells. This included 3 live species not previously observed in Lake Houston: *T. nobilis*, *T. texasiense*, and *L. lienosus*. The differences in species richness between our survey and other surveys in Lake Houston illustrates the value of increasing survey duration and area. For instance, the Burlakova et al. 2005 survey (Personal Communication) was 3 person-hours in duration, compared to our 44 person-hours. While the amount of area surveyed was not documented, it was likely far less than the 1.2 hectare we surveyed. In addition, Burlakova et al. may not have used SCUBA equipment or surveyed at depths greater than 1 meter. Total CPUE was similar for their survey and ours (24 and 32.8, respectively). Although total CPUE was lower for the Burlakova et al. (2005) survey, the highest CPUE they recorded for a single species (*Q. apiculata*) was 15.3, nearly twice as high as our value. In addition, their CPUE for *P. dombeyannus* (5.7) was also larger than our value of 4.02. In contrast, our CPUE for *C. pustulosa* (9.02) was larger than the Burlakova et al. (2005) CPUE of 1.0 for this species. We believe the ranges in CPUE values between the 2 surveys reflect differences in mussel distribution between the two survey areas rather than in mussel detection skills, and the increased number of species detected was due primarily to increased duration and area surveyed.

There appears to be no relationship between segment CPUE and segment species richness indicating that the number of different species present did not necessarily increase with increasing mussel density. We hypothesize that higher mussel density is occurring in the optimal habitat for the most abundant species, while increased species richness can be observed in areas that support both common and rarer species. The most common species observed within survey segments E, F, and G (the three segments with the highest CPUE values), in descending order of abundance were *C. pustulosa*, *Q. apiculata*, *T. nobilis*, and *P. dombeyannus*, which are also the 4 most abundant species within the entire survey area.

The presence of *T. nobilis* was unexpected (Figs. 5–6). The MoTX database has no records of this species for the San Jacinto Basin, and the nearest observation was approximately 65 kilometers north of Lake Houston, in the Trinity River Basin. However, Howells (2014) states the range of this species in Texas is from the San Jacinto River north and east to the Red River. It is possible this species has been overlooked, at least within Lake Houston, due to its apparent preference for deeper water. We did not observe *T. nobilis* within the shallower portion of the survey area, only at depths between 3.7 and 7.6 meters. Another unexpected species was *L. lienosus*, which was previously known from the upper sections of the East and West Forks of the San Jacinto River, with the closest observation to Lake Houston approximately 30 kilometers north on the East Fork.

Table 3. Summary of mussel species observations in the San Jacinto River system based on search of Mussels of Texas Database and the results of 2019 survey of site in Lake Houston, Harris County, TX.

Scientific Name	San Jacinto River (MoTX)	Lake Houston (MoTX)	2019 Lake Houston Survey	Notes (MoTX)	Most Recent Observation*
<i>Amblema plicata</i>	X	X	X		9/17/2015
<i>Arcidens confragosus</i>	X			One record	No Date
<i>Cyclonaias pustulosa</i>	X	X	X		10/7/2005
<i>Fusconaia chunii</i>	(East Fork Only)			One record	9/16/2016
<i>Fusconaia flava</i>	(East Fork Only)				7/27/2017
<i>Glebulia rotunda</i>	(West Fork Only)			One Record	7/31/1996
<i>Lampsilis hydiana</i>	X	X	X		10/7/2005
<i>Lampsilis satura</i>	(West Fork Only)				7/14/1979
<i>Lampsilis teres</i>	X	X	X		10/7/2005
<i>Leaunio lienosa</i>	(East Fork Only)		X		7/27/2017
<i>Leptodea fragilis</i>	X	X	X		10/7/2005
<i>Megalonaia nervosa</i>		X	X		10/7/2005
<i>Plectomerus dombeyanus</i>	X	X	X		10/7/2005
<i>Pleurobema riddellii</i>	(East Fork Only)				8/15/1986
<i>Potamilus purpuratus</i>	X	X	X		10/7/2005
<i>Pyganodon grandis</i>	X	X	X		10/7/2005
<i>Quadrula apiculata</i>	X	X	X		10/7/2005
<i>Strophitus undulatus</i>	(East Fork Only?)			One Record	No Date
<i>Toxolasma texasiense</i>	X		X		9/17/2015
<i>Tritogonia nobilis</i>			X		
<i>Tritogonia verrucosa</i>	(West Fork Only)			One Record	7/27/2009
<i>Truncilla truncata</i>	X	X	X		10/7/2005
<i>Utterbackia imbecillis</i>	X			One Record	7/14/1979
<i>Utterbackiana suborbiculata</i>		X	X	One Record	9/23/1982

\* Prior to 2019 Survey

The water quality of Lake Houston has long been a potential concern for the region. The lake is a major public water supply as well as a recreational lake used by the greater Houston metropolitan area (Sneck-Fahrer et al. 2005). The issues of concern for this waterbody stem from nutrient enrichment (phosphorus and nitrate / nitrite) loading and, for aquatic fauna, the amount of dissolved oxygen in the water (Sneck-Fahrer et al. 2005). Our results indicate that, despite impacts from damming and sediment deposition from frequent extreme floods, many of the freshwater mussel species found in other portions of the San Jacinto River are persisting and perhaps flourishing within Lake Houston. This mussel diversity may represent a significant ecological component of the lake, as mussels are foundational species that provide ecosystem services including food sources for numerous species (Haag 2012, Vaughn 2018). Based on 2018 bathymetry data (Leber et al. 2019), approximately 3,860 hectares of Lake Houston have a depth from zero to 7.9 meters. Based on our calculated overall mussel density for the entire survey area, and assuming that depth can be used as a surrogate for substrate as they relate to CPUE, we estimate there may be 3,783,486 or more mussels occupying the portion of Lake Houston with the same range of depths we surveyed (0 to 7.9 meters). This population estimate is only perfunctory and would benefit from additional sampling at various depths at other locations within the lake. Additional work is needed to ascertain mussel extent and diversity within Lake Houston. Additionally, extensive surveys should be carried out in other impoundments within the Sabine-Trinity Province in order to document the status of their mussel assemblages.

**Acknowledgments**

The authors acknowledge Ravi Kaleyatodi, Project Manager for the City of Houston’s Northeast Water Purification Plant (NEWPP) Expansion Project for obtaining authorization for publishing this

Table 4. Species observed during four surveys in Lake Houston between 1996 and 2019 including species represented by shells only.

Scientific Name	Common Name	1996a	1996b	2005	2019
<i>Amblema plicata</i>	Threeridge		X	X	X
<i>Cyclonaias pustulosa</i>	Pimpleback	X	X	X	X
<i>Lampsilis hydiana</i>	Louisiana Fatmucket		X	X	X
<i>Lampsilis teres</i>	Yellow Sandshell		X	X	X
<i>Leaunio lienosa</i>	Little Spectacle Case				X
<i>Leptodea fragilis</i>	Fragile Papershell		X	X	X
<i>Megaloniaias nervosa</i>	Washboard		X	X	X
<i>Plectomerus dombeyannus</i>	Bank Climber		X	X	X
<i>Potamilus purpuratus</i>	Bleufer		X	X	X
<i>Pyganodon grandis</i>	Giant Floater		X	X	X
<i>Quadrula apiculata</i>	Southern Mapleleaf	X	X	X	X
<i>Toxolasma texasiense</i>	Texas Lilliput				X
<i>Tritogonia nobilis</i>	Gulf Mapleleaf				X
<i>Truncilla truncata</i>	Deertoe			X	X
<i>Utterbackiana suborbiculata</i>	Flat Floater				X
Total Species		2	10	11	15



Figure 5. Top Photos: Two of the 130 live *Tritogonia nobilis* observed in Lake Houston in 2019, right photo shows more elongated form of older mussel. Bottom photo: interior view of shell of *T. nobilis*. Photos by S. Johnson.



Figure 6. Detail of collected shell of *Tritogonia nobilis* showing diagnostic paired rows of horizontal, shelf-like pustules from the beak to the margin on posterior slope. Photo by S. Johnson.



paper. We also acknowledge Paul Walker and Susan Berkey, both of Carollo Engineers, who are SWCA's immediate client and who represent the consulting engineer for the design and implementation of the multi-year water treatment infrastructure construction project. We wish to thank Jason Carlisle, Carollo's on-site construction coordinator, who assisted SWCA in obtaining site access and helped us stay safe during completion of our study. Finally, we wish to thank Heather Biggs, Chris Maldonado, Clint Robertson, Adam Whisenant, and Colleen Roco of TPWD who provided the appropriate state permits for this work and provided valuable suggestions and insight into our proposed sampling protocol and proposed freshwater mussel release sites.

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