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ARTICLE

THE KNOWN AND POTENTIAL HOSTS OF TEXAS MUSSELS: IMPLICATIONS FOR FUTURE RESEARCH AND CONSERVATION EFFORTS

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ABSTRACT

North America is home to the most diverse freshwater mussel fauna (Mollusca: Unionidae) in the world; however, at least 70% of native mussel species are considered imperiled to some degree. Texas has 52 currently recognized mussel species, and many of these have experienced significant population declines. These declines are anticipated to worsen as the population and water demands continue to grow throughout the state. The life history of unionids includes a unique reproductive strategy involving an obligate ectoparasitic larval stage; therefore, suitable host organisms are required for a mussel population to remain viable. Because of this relationship, the identification of host organisms is an important component for successful mussel conservation efforts. Data on host organisms are often difficult to locate or may be incomplete or completely lacking. We performed a comprehensive literature review to compile the known and/or potential host species for the mussels of Texas. Data was organized by mussel species and information including the total number of hosts identified in the literature review, type of host study methodology, and whether the mussel and/or host is a state or federally listed species was incorporated into a reference table. Identified host species were grouped by family, and the percentages for each host family were then compared for each mussel species using a chi-square goodness of fit analysis. The information compiled during this literature review exposes areas in need of future research and should be considered during the development of future mussel management and conservation protocols within Texas.

KEY WORDS - glochidia, unionid, mussel, host, fish, Texas, threatened

INTRODUCTION

North America is home to the most diverse freshwater bivalve fauna in the world, with the majority of species belonging to the Unionidae. Of the nearly 300 mussel species native to North America, approximately 70% are currently imperiled to some degree (Williams et al. 1993; Master et al. 2000; Lydeard et al. 2004; Strayer et al. 2004). Mussel declines have been attributed to the destruction and modification of their habitat, water withdrawal for human usage, pollution, droughts, and aquatic invasive species (Williams et al. 1993; Strayer et al. 2004; Bogan 2008; Haag 2012). In addition, freshwater mussels have a highly specialized life history, which makes them uniquely vulnerable to habitat disturbances. Adult mussels are relatively sedentary filter-feeders with reduced dispersal abilities and may remain in the same relative location during the majority of their adult lives (Kat 1984; Vaughn and Hakenkamp 2001). Their larvae (glochidia) are obligate parasites on the gills and/or fins of fish or more rarely, on amphibians (Kat 1984; Haag and Warren 1997).

Mussel host specificity varies among species and ranges from specialists that utilize only a few closely related host species, to generalists that use a wide variety of host species (Haag and Warren 1999). Currently, host species information is incomplete or completely lacking for a large number of mussel species in North America (Haag and Warren 1997), including many species found in Texas (Braun et al. 2014). Suitable freshwater mussel host organisms are typically identified through either laboratory or field-based studies, though most recent studies have primarily utilized laboratory-based methodology (Haag 2012; Levine et al. 2012).

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In laboratory-based studies, glochidia are exposed to potential host organisms under artificial conditions to observe whether or not attachment and metamorphosis occurs (Hove et al. 2011). If a high enough percentage of glochidia successfully metamorphose, then the species may be considered a usable host for the mussel species in question (Haag and Warren 1997; Sietman et al. 2010; Hove et al. 2011; Daniel and Brown 2012). However, these types of studies circumvent the natural behavioral and ecological obstacles that may inhibit a mussel species from utilizing a potential host organism. Often laboratory-based studies fail to consider crucial life history traits of the host and mussel species as well as other environmental factors that may influence the infection rate, survival, and transformation of glochidia (Levine et al. 2012). Because of these limitations, laboratory-based studies have the potential to over-represent the taxonomic breadth of the host organisms naturally available to a mussel species (Levine et al. 2012).

Field-based studies for identifying a host organism involve the capture of infected hosts in a natural ecological setting (Hove et al. 2011). Captured hosts are either held in the laboratory until the glochidia metamorphose into juvenile mussels, or the gills and/or fins of the host are removed and searched for encysted glochidia (Zale and Neves 1982; Hove and Neves 1994; Boyer et al. 2011). Studies such as these indicate the natural infection of a host organism and identify a potential host species that interacts with a mussel species in a natural ecological setting (Hove et al. 2011). Field-based studies also have potential limitations. For example, glochidia have the potential to remain attached to inanimate objects and non-suitable hosts for a period of time (Haag 2012); therefore, a natural infection may not necessarily indicate that the purported host organism is usable. In addition, not all host species are likely to be obtained during field collections, such as those host species too small to notice or to be easily located (Levine et al. 2012) or those species that are used as host organisms by a mussel species which releases its glochidia during a time other than when collections occurred.

Host identification is critical to the success of future freshwater mussel conservation, management, and propagation endeavors (Burlakova et al. 2011; Daniel and Brown 2012; Johnson et al. 2012; Levine et al. 2012). Texas has 52 currently recognized species of native freshwater mussels. One of these species is federally listed as endangered, and 15 species are listed as threatened at the state level. Of the state-listed species, six are also currently listed as candidates for further federal protection, and six have been petitioned for a federal listing and have received positive 90-day findings (USFWS 2011a). To assist in future research prioritizations, mussel and fish conservation management, and potential water management evaluations, we performed an extensive review of the available mussel host literature. This information was then combined into a database indicating the host species for Texas' mussels.

METHODS

An extensive literature review was conducted to compile the known and/or potential host species for the mussels of Texas. Only those sources which identified host organisms to the species level were used to create Table 1. Both native and non-native fish were included as host organisms in Table 1, provided that the non-native species had an established and reproducing population in Texas (Howells 2001b; Thomas et al. 2007; Hendrickson and Cohen 2012). Both laboratory and field-based studies were included in this literature review. Species determined to not serve as hosts for a given species were not included in Table 1.

Table 1 is organized by mussel species, and information including the total number of hosts identified in the literature review, whether the mussel is a state or federally listed species, and whether the host is a state or federally listed or non-native species was incorporated into the "Species" column. To identify the source of the host species information, numbers were included under the "Host Species" column in Table 1 which correspond with numbers added to the sources in the Literature Cited section. In addition, the type of study for each source used to create Table 1 is included in the Literature Cited section. Each source is categorized by a two-letter code devised by Hoggarth (1992) and included LI (laboratory infestation; host parasitized in experimental conditions but metamorphosis not observed), LT (laboratory infestation; host parasitized in experimental conditions and metamorphosis observed), NI (natural infestation; parasite found on wild-caught fish but metamorphosis not observed), NT (natural infestation; parasite found on wild-caught fish and metamorphosis observed), and NS (not stated in original source). Both the LI and LT categories were classified as laboratory-based studies and the NI and NT categories were classified as field-based studies.

For each mussel species, identified host species were grouped by family, and the total percentage that each host family was utilized by a mussel species was calculated. These percentages were included in Table 1. The percentages for each host family were then compared for each mussel species using a chi-square goodness of fit analysis. A significant value for this analysis indicates that a mussel species was found more often on a host in a particular family than would be expected by random chance. This information was also included in Table 1 within the "Species" column.

Table 2 includes information regarding the number of host species per family as determined by the literature review. Texas mussel species with no available host data are shown in Table 3 with their corresponding state and/or federal listing status.

RESULTS & DISCUSSION

The literature review identified a total of 95 known and/or potential host organisms for at least one Texas mussel species (Tables 1, 2). Of the 89 papers used as sources for Table 1,

Table 1. The known and/or potential host species for the unionids of Texas. The total number of known and/or potential host organisms used by a mussel species is shown in parentheses.

Species	Host Family	Total Hosts	% of Total	Host Species
Amblema plicata^{+} (21)	Catostomidae	1	4.8%	*Moxostoma erythrurum*[85, 86]
	Centrarchidae	8	38.1%	*Ambloplites rupestris**[15,16,37,86], *Lepomis cyanellus*[15,16,37,86], *Lepomis gulosus*[8,15,16,28,37], *Lepomis macrochirus*[15,16,28,37,85,86], *Lepomis megalotis*[43,49,86], *Micropterus salmoides*[8,15,16,28,37,46,86], *Pomoxis annularis*[8,15,16,28,37,63,86,87], *Pomoxis nigromaculatus*[8,15,16,28,37,46,86]
	Cyprinidae	3	14.3%	*Cyprinella lutrensis*[49], *Cyprinella venusta*[49], *Notropis atherinoides*[85,86]
	Ictaluridae	2	9.5%	*Ictalurus punctatus*[14,15,28,37,64,85,86], *Pylodictis olivaris*[14,15,16,28,37,64]
	Lepisosteidae	2	9.5%	*Lepisosteus oculatus*[43,86], *Lepisosteus platostomus*[8,15,16,29,37]
	Moronidae	1	4.8%	*Morone chrysops*[8,15,16,37,86,87]
	Percidae	3	14.3%	*Perca flavescents**[8,16,28,37,46,83,86], *Percina caprodes*[85,86], *Sander canadensis**[8,15,16,28,37,63,86,87]
	Sciaenidae	1	4.8%	*Aplodinotus grunniens*[36,85,86]
Anodonta suborbiculata^{+} (8)	Centrarchidae	5	62.5%	*Lepomis cyanellus*[34,86], *Lepomis gulosus*[3,4,34,86], *Lepomis megalotis*[34,86], *Micropterus salmoides*[3,4,34,36,86], *Pomoxis annularis*[3,4,34,36,86]
	Cyprinidae	1	12.5%	*Notemigonus crysoleucas*[3,4,34,36,86]
	Ictaluridae	1	12.5%	*Ictalurus punctatus*[34,36,64,86]
	Poeciliidae	1	12.5%	*Gambusia affinis*[36]
Arcidens confragosus^{+} (21)	Anguillidae	1	4.8%	*Anguilla rostrata*[15,37,86,87]
	Catostomidae	4	19.0%	*Carpiodes cyprinus*[70], *Erimyzon oblongus*^{X}[70], *Ictiobus bubalus*[70], *Moxostoma macrolepidotum*[25,70]
	Centrarchidae	4	19.0%	*Ambloplites rupestris**[15,37,63,86,87], *Lepomis cyanellus*[34,70], *Lepomis humilis*[70], *Pomoxis annularis*[15,37,63,86,87]
	Clupeidae	1	4.8%	*Dorosoma cepedianum*[15,37,63,86,87]
	Cyprinidae	5	23.8%	*Cyprinus carpio**[25], *Luxilus chrysocephalus*[70], *Notemigonus crysoleucas*[70], *Rhinichthys cataractae*[70], *Semotilus atromaculatus*[25,70]
	Fundulidae	1	4.8%	*Fundulus olivaceous*[70]
	Ictaluridae	1	4.8%	*Ictalurus punctatus*[34,36,37,64,70,86]
	Percidae	2	9.5%	*Perca flavescens**[25], *Sander vitreus**[36,70]
	Poecilliidae	1	4.8%	*Poecilia reticulata**[70]
	Sciaenidae	1	4.8%	*Aplodinotus grunniens*[37,86,87]
Arkansia wheeleri^{X} (1)	Cyprinidae	1	100.0%	*Lythrurus umbratilis*[68]
Cyrtonaias tampicoensis^{+} (5)	Centrarchidae	1	20.0%	*Lepomis megalotis*[36]
	Cichlidae	1	20.0%	*Herichthys cyanoguttatum* [35,36]
	Cyprinidae	1	20.0%	*Notemigonus crysoleucas*[35,36]
	Lepisosteidae	2	40.0%	*Lepisosteus oculatus*[35], *Lepisosteus osseus*[34,35,36]

approximately 65% (58 sources of the LT and/or LI categories) were laboratory-based studies, 12% (11 sources of the NI category) were field-based studies, and 14% (12 sources of the NS category) did not state host species determination methodology. The remaining 9% (8 sources) included both laboratory and field-based investigations, and notably, only four of these studies were conducted after 1975.

From the literature review, a total of 95 host species from 24 different host families were identified (Tables 1, 2). Of these 95 host species identified, 92 are a species of fish and three are a species of amphibian. The majority of host species (61%) were from four families, including the Cyprinidae (22.1%, 21 host species), Centrarchidae (16.5%, 16 host species), Percidae (12.4%, 12 host species), or Ictaluridae (9.5%, 9 host species). In addition, 15 of the 24 host families (16.5%) had only a single species utilized as a host (Table 2).

Table 1, continued.

Species	Host Family	Total Hosts	% of Total	Host Species
Elliptio dilatata^{+} (23)	Anguillidae	1	4.3%	*Anguilla rostrate*[58]
	Centrarchidae	8	34.8%	*Ambloplites rupestris**[12,16,58,86], *Lepomis cyanellus*[58], *Lepomis macrochirus*[58], *Lepomis megalotis*[58], *Micropterus dolomieu**[58], *Micropterus salmoides*[12,58], *Pomoxis annularis*[12,14,15,16,28,37,86,87], *Pomoxis nigromaculatus*[12,14,15,16,28,37,58,86]
	Clupeidae	1	4.3%	*Dorosoma cepedianum*[12,14,15,16,37,86,87]
	Cyprinidae	2	8.7%	*Notemigonus crysoleucas*[58], *Rhinichthys cataractae*[58]
	Fundulidae	1	4.3%	*Fundulus olivaceus*[58]
	Ictaluridae	1	4.3%	*Pylodictis olivaris*[12,14,15,16,28,37,64,86]
	Lepisosteidae	1	4.3%	*Lepisosteus osseus*[58]
	Percidae	8	34.8%	*Etheostoma caeruleum*[12,16,58,86], *Perca flavescens**[12,14,16,37,58,86], *Percina caprodes*[58], *Percina maculata*^{X}[58], *Percina phoxocephala*[58], *Percina shumardi*[58], *Sander canadensis**[12,28,58,86], *Sander vitreus**[58]
Fusconaia askewi^{X+} (17)	Centrarchidae	3	17.7%	*Lepomis macrochirus*[49], *Lepomis megalotis*[49], *Micropterus punctulatus*[49]
	Clupeidae	1	5.9%	*Dorosoma cepedianum*[49]
	Cyprinidae	7	41.2%	*Cyprinella lutrensis*[49], *Cyprinella venusta*[49], *Hybopsis ammis*[49], *Notemigonus crysoleucas*[49], *Notropis texanus*[49], *Pimephales promelas*[49], *Pimephales vigilax*[49]
	Esocidae	1	5.9%	*Esox americanus*[49]
	Fundulidae	1	5.9%	*Fundulus notatus*[49]
	Ictaluridae	2	11.8%	*Ictalurus punctuatus*[49], *Noturus nocturnus*[49]
	Percidae	1	5.9%	*Percina sciera*[49]
	Poeciliidae	1	5.9%	*Gambusia affinis*[49]
Fusconaia flava^{+} (4)	Centrarchidae	3	75.0%	*Lepomis macrochirus*[14,15,16,28,36,37], *Pomoxis annularis*[8,14,15,16,28,36,37,87], *Pomoxis nigromaculatus*[8,14,15,16,28,36,37,63,87]
	Cyprinidae	1	25.0%	*Semotilus atromaculatus*[16,50,74]
Glebula rotundata (7)	Achiridae	1	14.3%	*Trinectes maculatus*[36,37,53,86]
	Centrarchidae	2	28.6%	*Lepomis cyanellus*[36,37,53,86], *Lepomis macrochirus*[36,37,53,86]
	Cyprinidae	1	14.3%	*Cyprinus carpio**[36,37,53,86]
	Engraulidae	1	14.3%	*Anchoa mitchilli*[36,37,53,86]
	Lepisosteidae	1	14.3%	*Lepisosteus oculatus*[36,37,53,86]
	Moronidae	1	14.3%	*Morone chrysops*[36,37,53,86]
Lampsilis bracteata^{X} (4)	Centrarchidae	4	100.0%	*Lepomis cyanellus*[34,36,37,40], *Lepomis macrochirus*[34,36,37,40], *Micropterus salmoides*[36,40], *Micropterus treculii*[36,40]
Lampsilis cardium^{+} (12)	Ambystomatidae	1	8.3%	*Ambystoma tigrinum*[36,73,75,76]
	Centrarchidae	6	50.0%	*Lepomis cyanellus*[16,50,72], *Lepomis macrochirus*[8,15,16,37,69], *Micropterus dolomieu**[8,15,16,37,69], *Micropterus salmoides*[8,11,15,16,46,69,76,81], *Pomoxis annularis*[2,8,15,16,37,69,87], *Pomoxis nigromaculatus*[11]
	Percidae	3	25.0%	*Perca flavescens**[8,16,69], *Sander canadensis**[2,8,15,16,37,69,87], *Sander vitreus**[16,41,69,87]
	Poeciliidae	2	16.7%	*Poecilia reticulata**[75,76], *Xiphophorus hellerii**[75,76]
Lampsilis hydiana^{+} (3)	Centrarchidae	1	33.3%	*Lepomis cyanellus*[34,36]
	Ictaluridae	2	66.7%	*Ictalurus furcatus*[34,36,64], *Ictalurus punctatus*[34,36,64]

Table 1, continued.

Species	Host Family	Total Hosts	% of Total	Host Species
Lampsilis satura[X] (1)	Centrarchidae	1	100.0%	*Lepomis macrochirus*[31,32]
Lampsilis teres[+] (21)	Acipenseridae	1	4.8%	*Scaphirhynchus platorynchus*[X36,37,63,86,87]
	Centrarchidae	12	57.1%	*Lepomis auritus**[56,86], *Lepomis cyanellus*[15,37,63,86], *Lepomis gulosus*[15,37,63,86,87], *Lepomis humilis*[9,15,37,63,86], *Lepomis macrochirus*[43,46,56,86], *Lepomis marginatus*[43], *Lepomis megalotis*[43], *Lepomis microlophus*[9], *Micropterus punctulatus**[43], *Micropterus salmoides*[9,15,36,37,42,43,63,86,87], *Pomoxis annularis*[9,15,37,63,86,87], *Pomoxis nigromaculatus*[15,37,63,86]
	Cyprinidae	1	4.8%	*Cyprinella venusta*[9,43]
	Lepisosteidae	4	19.1%	*Lepisosteus oculatus*[43], *Lepisosteus osseus*[1,8,15,37,42,87], *Lepisosteus platostomus*[8,15,29,37,42,86,87], *Lepisosteus spatula*[8,37,86,87]
	Percidae	3	14.3%	*Etheostoma lepidum*[56,86], *Etheostoma stigmaeum*[43], *Perca flavescens**[46]
Lasmigona complanata[+] (10)	Catostomidae	1	10.0%	*Moxostoma congestum*[85]
	Centrarchidae	4	40.0%	*Lepomis cyanellus*[15,16,37,46,51,86,89], *Lepomis humilis*[16,51,86,89], *Micropterus salmoides*[15,16,37,44,51,86,89], *Pomoxis annularis*[15,16,37,44,46,51,86,89]
	Clupeidae	1	10.0%	*Dorosoma cepedianum*[85,86]
	Cyprinidae	2	20.0%	*Cyprinus carpio**[15,16,37,44,46,86], *Notemigonus crysoleucas*[51]
	Lepisosteidae	1	10.0%	*Lepisosteus osseus*[85,86]
	Percidae	1	10.0%	*Sander canadensis**[85,86]
Leptodea fragilis (1)	Sciaenidae	1	100.0%	*Aplodinotus grunniens*[14,15,16,27,29,36,37,60,86,87]
Ligumia subrostrata (5)	Centrarchidae	5	100.0%	*Lepomis cyanellus*[14,36,37,46,62,86], *Lepomis gulosus*[36,62,86], *Lepomis humilis*[14,36,37,46,86], *Lepomis macrochirus*[14,36,37,62,86], *Micropterus salmoides*[14,36,37,46,86]
Megalonaias nervosa[+] (29)	Acipenseridae	1	3.5%	*Scaphirhynchus platorynchus*[X84]
	Amiidae	1	3.5%	*Amia calva*[15,28,36,37,86]
	Angullidae	1	3.5%	*Anguilla rostrata*[8,15,37,86,87]
	Centrarchidae	8	27.6%	*Lepomis cyanellus*[8,28,51,84,86,88], *Lepomis gulosus*[85,86], *Lepomis macrochirus*[8,15,28,37,50,51,77,86], *Lepomis megalotis*[43,50,51,77,86], *Micropterus punctulatus*[85,86], *Micropterus salmoides*[15,28,37,42,50,51,77,84,86], *Pomoxis annularis*[8,15,28,37,51,85,86], *Pomoxis nigromaculatus*[8,15,28,37,86]
	Clupeidae	2	6.9%	*Alosa chrysochloris*[8,15,37,86,87], *Dorosoma cepedianum*[8,15,28,37,85,86]
	Cyprinidae	2	6.9%	*Campostoma anomalum*[51,77,86], *Notemigonus crysoleucas*[84]
	Ictaluridae	6	20.7%	*Ameiurus melas*[8,15,28,37,51,64,84,86,88], *Ameiurus natalis*[64,84], *Ameiurus nebulosus*[8,15,37,51,64,86], *Ictalurus punctatus*[8,15,28,37,51,64,86,88], *Noturus gyrinus*[8,37,64,86], *Pylodictis olivaris*[8,15,28,37,64,85,86]
	Lepisosteidae	2	6.9%	*Lepisosteus oculatus*[43], *Lepisosteus osseus*[50,77,85,86]
	Moronidae	1	3.5%	*Morone chrysops*[8,15,28,37,51,85,86,87]
	Percidae	4	13.8%	*Perca flavescens**[50,51,77,86], *Percina caprodes*[50,77,86], *Percina phoxocephala*[50,77,86], *Sander canadensis**[15,28,37]

Table 1, continued.

Species	Host Family	Total Hosts	% of Total	Host Species
	Sciaenidae	1	3.5%	*Aplodinotus grunniens*[8,15,28,36,37,51,63,85,87]
Obliquaria reflexa+ (9)	Centrarchidae	4	44.4%	*Lepomis megalotis*[43], *Lepomis miniatus*[43], *Micropterus punctulatus*[43], *Micropterus salmoides*[43]
	Cyprinidae	3	33.3%	*Cyprinella venusta*[43], *Luxilus chrysocephalus*[78], *Rhinichthys cataractae*[36,78,80,86]
	Lepisosteidae	1	11.1%	*Lepisosteus oculatus*[43]
	Percidae	1	11.1%	*Etheostoma stigmaeum*[43]
Plectomerus dombeyanus (2)	Cyprinidae	1	50.0%	*Cyprinella lutrensis*[49]
	Fundulidae	1	50.0%	*Fundulus notatus*[49]
*Pleurobema riddellii*X (2)	Cyprinidae	2	100.0%	*Cyprinella lutrensis*[49], *Pimephales vigilax*[49]
*Popenaias popeii*X+ (28)	Catostomidae	3	10.7%	*Carpiodes carpio*[5,36,47], *Cycleptus elongatus*X[5,47], *Moxostoma congestum*[5,36,47]
	Centrarchidae	5	17.9%	*Lepomis cyanellus*[5,47], *Lepomis macrochirus*[5,47], *Lepomis megalotis*[5,47], *Micropterus punctulatus*[47], *Micropterus salmoides*[5,47]
	Characidae	1	3.6%	*Astyanax mexicanus*[5,35,47]
	Cichlidae	1	3.6%	*Herichthys cyanoguttatum*[5,35]
	Clupeidae	1	3.6%	*Dorosoma cepedianum*[5]
	Cyprinidae	8	28.6%	*Campostoma anomalum*[5,47], *Cyprinella lutrensis*[5,47], *Cyprinus carpio**[5,47], *Dionda episcopa*[5,47], *Hybognathus placitus*[5,47], *Macrhybopsis aestivalis*[5,47], *Notropis jemezanus*[5,47], *Pimephales promelas*[5,47]
	Fundulidae	2	7.1%	*Fundulus zebrinus*[5,47], *Lucania parva*[5,47]
	Ictaluridae	4	14.3%	*Ameiurus natalis*[5,47], *Ictalurus lupus*[47], *Ictalurus punctatus*[5,47], *Pylodictis olivaris*[47]
	Lepisosteidae	1	3.6%	*Lepisosteus osseus*[5,35,47]
	Percidae	1	3.6%	*Etheostoma lepidum*[5,35,47]
	Poeciliidae	1	3.6%	*Gambusia affinis*[5,35,47]
Potamilus ohiensis (3)	Centrarchidae	1	33.3%	*Pomoxis annularis*[15,27,36,37,63,86,87]
	Fundulidae	1	33.3%	*Fundulus notatus*[15]
	Sciaenidae	1	33.3%	*Aplodinotus grunniens*[15,16,27,29,36,37,60,63,86,87]
Potamilus purpuratus+ (4)	Centrarchidae	1	25.0%	*Lepomis gulosus*[30,86]
	Cyprinidae	2	50.0%	*Cyprinella lutrensis*[49], *Notemigonus crysoleucas*[30,86]
	Sciaenidae	1	25.0%	*Aplodinotus grunniens*[29,35,36,37,63,86,87]
Pyganodon grandis+ (33)	Atherinopsidae	1	3.0%	*Labidesthes sicculus*[15,37,65,86]
	Catostomidae	1	3.0%	*Carpiodes carpio*[6]
	Centrarchidae	8	24.2%	*Ambloplites rupestris**[15,37,44,65,67,86], *Lepomis cyanellus*[15,37,65,67,86,87], *Lepomis humilis*[1,86], *Lepomis macrochirus*[6,15,37,44,54,65,81,86,87], *Lepomis megalotis*[15,37,54,86], *Micropterus salmoides*[6,15,37,54,65,81,86,87], *Pomoxis annularis*[6,15,37,44,81,86,87], *Pomoxis nigromaculatus*[15,37,65,86,87]
	Cichlidae	1	3.0%	*Herichthys cyanoguttatum*[34,86]
	Clupeidae	2	6.1%	*Alosa chrysochloris*[15,37,63,86,87], *Dorosoma cepedianum*[15,37,63,86,87]

Table 1, continued.

Species	Host Family	Total Hosts	% of Total	Host Species
	Cyprinidae	8	24.2%	*Campostoma anomalum*[15,37,65,86], *Carassius auratus**[81,86], *Cyprinus carpio**[6,15,37,44,86], *Luxilus chrysocephalus*[44,57,65], *Lythrurus umbratilis*[15,37,65,86], *Notemigonus crysoleucas*[15,37,44,65,86], *Pimephales notatus*[15,37,65,86], *Semotilus atromaculatus*[37,65,81,86]
	Fundulidae	1	3.0%	*Fundulus chrysotus*[54,86]
	Ictaluridae	2	6.1%	*Ameiurus natalis*[15,37,64,86,87], *Ameiurus nebulosus*[37,86]
	Lepisosteidae	2	6.1%	*Lepisosteus osseus*[15,37,65,86], *Lepisosteus spatula*[15,37,87]
	Moronidae	1	3.0%	*Morone chrysops*[15,86,87]
	Percidae	3	9.1%	*Etheostoma caeruleum*[15,37,65,86], *Perca flavescens**[37,38,39,44,65,86], *Sander vitreus**[41]
	Poeciliidae	2	6.1%	*Gambusia affinis*[86], *Poecilia reticulata**[81,86]
	Sciaenidae	1	3.0%	*Aplodinotus grunniens*[15,36,37,86,87]
Quadrula mortoni^{+} (5)	Centrarchidae	3	60.0%	*Lepomis megalotis*[49], *Micropterus punctulatus*[49], *Micropterus salmoides*[49]
	Clupeidae	1	20.0%	*Dorosoma cepedianum*[49]
	Cyprinidae	1	20.0%	*Cyprinella lutrensis*[49]
Quadrula nobilis (2)	Ictaluridae	2	100.0%	*Ictalurus punctatus*[33,34,36,64,86], *Pylodictis olivaris*[33,34,36,64,86]
Quadrula nodulata (9)	Centrarchidae	4	44.4%	*Lepomis macrochirus*[14,15,28,37], *Micropterus salmoides*[14,15,28,37], *Pomoxis annularis*[8,15,37,61,63,87], *Pomoxis nigromaculatus*[14,15,28,37]
	Ictaluridae	5	55.6%	*Ameiurus melas*[36,61], *Ameiurus nebulosus*[36,61], *Ictalurus furcatus*[36,61], *Ictalurus punctatus*[8,14,15,37,61,64,87], *Pylodictis olivaris*[8,14,15,37,61,64]
Quadrula pustulosa^{+} (6)	Acipenseridae	1	16.7%	*Scaphirhynchus platorynchus*[X][8,14,16,37,86]
	Centrarchidae	1	16.7%	*Pomoxis annularis*[14,15,16,37,63,86,87]
	Ictaluridae	4	66.7%	*Ameiurus melas*[8,14,15,16,27,28,36,37,64,86], *Ameiurus nebulosus*[8,14,15,16,28,36,37,64,86], *Ictalurus punctatus*[8,14,15,16,27,28,29,36,37,64,85,86], *Pylodictis olivaris*[8,14,15,16,27,28,36,37,64,86,87]
Quadrula quadrula (4)	Centrarchidae	2	50.0%	*Lepomis cyanellus*[16,71], *Lepomis megalotis*[16,71]
	Ictaluridae	2	50.0%	*Ictalurus punctatus*[16,36,59,64,86], *Pylodictis olivaris*[15,16,29,37,59,64,86]
Quadrula verrucosa^{+} (6)	Cyprinidae	1	16.7%	*Notropis texanus*[49]
	Ictaluridae	3	50.0%	*Ameiurus natalis*[26,36,55,64,86], *Ameiurus nebulosus*[23,26,36,64,86], *Pylodictis olivaris*[24,26,33,34,36,64,86]
	Percidae	1	16.7%	*Etheostoma asprigene*[49]
	Poeciliidae	1	16.7%	*Gambusia affinis*[49]
Strophitus undulatus^{+} (28)	Centrarchidae	9	32.1%	*Ambloplites rupestris**[17,18,86], *Lepomis auritus**[13], *Lepomis cyanellus*[7,13,14,15,16,37,86], *Lepomis macrochirus*[7,13,16,19,22,86], *Lepomis microlophus*[81,86], *Micropterus dolomieu**[7,86], *Micropterus salmoides*[2,7,15,16,17,18,19,22,37,86], *Pomoxis annularis*[78,79,86], *Pomoxis nigromaculatus*[7,86]
	Cyprinidae	6	21.4%	*Campostoma anomalum*[7,18,86], *Notropis stramineus*[78,79,86], *Pimephales notatus*[7,78,79,86], *Pimephales promelas*[7,16,19,22,86], *Rhinichthys cataractae*[7,17,18,78,79,86], *Semotilus atromaculatus*[2,7,15,16,37,86]
	Fundulidae	1	3.6%	*Fundulus zebrinus*[14,86]

Table 1, continued.

Species	Host Family	Total Hosts	% of Total	Host Species
	Ictaluridae	4	14.3%	*Ameiurus melas*[7,16,19,22,64,86], *Ameiurus natalis*[7,16,18,19,22,64,86], *Ameiurus nebulosus*[82], *Ictalurus punctatus*[7,64,86]
	Percidae	6	21.4%	*Etheostoma caeruleum*[7,81,86], *Perca flavescents**[7,17,18,86], *Percina caprodes*[7,82,86], *Percina maculata*[X][7,86], *Percina phoxocephala*[7,86], *Sander vitreus**[16,19,22,86]
	Salamandridae	1	3.6%	*Notophthalmus viridescens*[18,86]
	Salmonidae	1	3.6%	*Oncorhynchus mykiss**[18,86]
	Transformation without a host[29,45,46,67,86]			
Toxolasma parvum (6)	Centrarchidae	6	100.0%	*Lepomis cyanellus*[14,16,20,37,48,71,86], *Lepomis gulosus*[15,16,37,48,71,86,87], *Lepomis humilis*[14,16,37,48,71,86], *Lepomis macrochirus*[16,37,48,71,83,86], *Micropterus salmoides*[71], *Pomoxis annularis*[14,16,37,48,71,86]
Toxolasma texasensis (3)	Centrarchidae	3	100.0%	*Lepomis gulosus*[36,37,62], *Lepomis macrochirus*[36,62], *Lepomis megalotis*[36,37,62]
Truncilla donaciformis (2)	Percidae	1	50.0%	*Sander canadensis**[15,16,36,37,63,86,87]
	Sciaenidae	1	50.0%	*Aplodinotus grunniens*[15,16,22,27,29,36,37,60,63,86,87]
Truncilla truncata (2)	Percidae	1	50.0%	*Sander canadensis**[14,15,16,36,37,86,87]
	Sciaenidae	1	50.0%	*Aplodinotus grunniens*[14,15,16,29,36,37,49,60,86,87]
Uniomerus tetralasmus (1)	Cyprinidae	1	100.0%	*Notemigonus crysoleucas*[16,35,36,37,62,86]
Utterbackia imbecillis[+] (20)	Ambystomatidae	1	5.0%	*Ambystoma tigrinum*[75,76]
	Centrarchidae	8	40.0%	*Ambloplites rupestris**[15,37,65,86], *Lepomis cyanellus*[15,37,65,66,67,86], *Lepomis gulosus*[15,37,62,86], *Lepomis macrochirus*[15,37,42,62,65,83,86], *Lepomis marginatus*[37,62,86], *Lepomis megalotis*[15,52,86], *Micropterus salmoides*[15,37,42,65,76,86], *Pomoxis nigromaculatus*[21,86]
	Cyprinidae	4	20.0%	*Carassius auratus**[75,76], *Luxilus chrysocephalus*[83], *Notemigonus crysoleucas*[42,86], *Semotilus atromaculatus*[6,14,15,37,86]
	Ictaluridae	1	5.0%	*Ictalurus punctatus*[42,64,86]
	Percidae	2	10.0%	*Etheostoma lepidum*[34,37,86], *Perca flavescens**[37,65,86]
	Poeciliidae	3	15.0%	*Gambusia affinis*[15,37,62,86], *Poecilia reticulata**[75,76], *Xixphophorus hellerii**[75,76]
	Ranidae	1	5.0%	*Rana catesbeiana*[75,76]
	Transformation without a host[10,29,36,37,67,86]			
Villosa lienosa[+] (12)	Centrarchidae	8	66.7%	*Lepomis cyanellus*[9], *Lepomis humilis*[9], *Lepomis macrochirus*[9,36,42,43,86], *Lepomis marginatus*[43], *Lepomis megalotis*[9,43], *Lepomis microlophus*[9], *Micropterus punctulatus*[43], *Micropterus salmoides*[9,36,42,86]
	Cyprinidae	1	8.3%	*Cyprinella venusta*[43]
	Ictaluridae	2	16.7%	*Ameiurus nebulosus*[36,64,86], *Ictalurus punctatus*[36,42,64,86]
	Lepisosteidae	1	8.3%	*Lepisosteus oculatus*[43]

* - A non-native fish species.

[X] - A state or federally-listed species.

[+] - Unequal ($P<0.05$) host family usage by a mussel species.

Four state-listed threatened fish species were identified as hosts, including *Percina maculata*, a host for *Quadrula verrucosa* and *Strophitus undulatus*; *Erimyzon oblongus*, a host for *Arcidens confragosus*; *Scaphirhynchus platorynchus*, a host for *Lampsilis teres*, *Megalonaias nervosa*, and *Quadrula pustulosa*; and *Cycleptus elongates*, a host for *Popenaias popeii*, which is also state-threatened (Table 1). Several non-native fish species known to occur in Texas were identified as hosts for Texas mussels, including *Perca flavescens*, *Cyprinus carpio*, and *Poecilia reticulata*, which are hosts to nine, five, and four mussel species, respectively (Table 1).

Table 2. The host families and the number of host species of each family utilized by the mussels of Texas.

Host Family	Total Species Utilized	% Host Family is Utilized
Achiridae	1	1.1%
Acipenseridae	1	1.1%
Ambystomatidae*	1	1.1%
Amiidae	1	1.1%
Anguilidae	1	1.1%
Atherinopsidae	1	1.1%
Catostomidae	8	8.2%
Centrarchidae	16	16.5%
Characidae	1	1.1%
Cichlidae	1	1.1%
Clupeidae	2	2.1%
Cyprinidae	21	22.1%
Engraulidae	1	1.1%
Esocidae	1	1.1%
Fundulidae	5	5.3%
Ictaluridae	9	9.5%
Lepisosteidae	4	4.2%
Moronidae	1	1.1%
Percidae	12	12.4%
Poeciliidae	3	3.2%
Ranidae*	1	1.1%
Salamandridae*	1	1.1%
Salmonidae	1	1.1%
Sciaenidae	1	1.1%
Total	**95**	**100%**

* - An amphibian species.

The vast majority of host studies to date have focused on fish species, with little research conducted on amphibian species as hosts for mussels. From the literature review, three mussel species were found to utilize amphibian larvae as hosts, specifically, *Lampsilis cardium* utilizes *Ambystoma tigrinum*; *S. undulatus* utilizes *Notophthalmus viridenscens*; and *Utterbackia imbecillis* utilizes both *A. tigrinum* and *Rana catesbeiana* (Table 1). The literature review also revealed evidence that the glochidia of two Texas mussel species, *S. undulatus* and *U. imbecillis,* can metamorphose into juvenile mussels without the use of a host (Table 1), instead the glochidia transformed while still within the female and were released as full formed juvenile mussels. Notably, both mussel species also utilize a fairly wide range of host organisms including amphibians and non-native fish species (Table 1).

Of Texas' 52 mussel species, 39 had some host data available (Table 1). The chi-square goodness of fit analysis indicated that 22 mussel species used a particular host family significantly more than other host families (Table 1). For example, we found that *Anodonta suborbiculata* utilized Centrarchidaes as hosts significantly more than any of its other known host families. Only seven mussel species utilized host families evenly, and the remaining ten mussel species only had host data available for host species from a single family (Table 1). It should be noted that these host family preferences were calculated using only the host data currently available in the literature and may not indicate a true preference for a host family by the mussel species in a natural setting. The indication of a preferred host family could have been caused by bias in the research toward a particular host family or the lack of available data regarding all host species utilized by a particular mussel species; therefore, as more host species research is conducted, host family preferences indicated within Table 1 are likely to be modified.

Because laboratory studies often over estimate the number of hosts usable by a mussel species (Levine et al. 2012) and the majority (65%) of available sources were laboratory-based studies, it is important to note that future studies for Texas mussel host identification may not support all findings compiled in Table 1. Additionally, there are likely other species utilized as hosts for mussels in Texas that have not yet been investigated, especially those species which are rare and/or endemic to Texas (Table 1).

Because of the limitations relating to laboratory and field-based studies, neither type of study alone is likely to provide a complete picture of the host species utilized by a mussel species in a natural setting (Levine et al. 2012). Due to these limitations, it is ideal that a combination of these studies be utilized when attempting to confirm host species. For example, it is recommended that laboratory-based studies conducted to demonstrate whether an organism may be used as a host be followed with field-based studies to further verify that the host in question is utilized by the mussel species in a natural setting. Conversely, it is recommended that researchers observe the transformation of glochidia on wild-caught fish, rather than determining the species to be a useable host simply based on the presence of glochidia.

Of the 13 mussel species in Texas with no available host data, ten of these are state threatened species (Table 3). Very little life history information of any kind was available for the majority of Texas' state threatened mussel species, though some data was available for *P. popeii* (Carman 2007; Levine et al. 2012). Typically, reports and papers only indicate locations where state-listed threatened species have been found along with some generalized habitat information, but do not expand in depth on life history information (Howells 1995; Howells 1996a, 1996b, 1997a, 1998, 1999, 2000, 2001a, 2002a, 2003, 2004, 2005, 2006, 2010; Howells et al. 1996; Bordelon and Harrel 2004; Karatayev and Burlakova 2007, 2008; Ford et al. 2009, 2010; Randklev et al. 2009, 2011; Burlakova and Karatayev 2010; Perry et al. 2010; Burlakova et al. 2011). Though occurrence information is essential for determining those locations in need of conservation, extensive research into the life histories of state-listed threatened mussels in Texas is crucial if conservation efforts are to be successful.

As previously discussed, ten of the 15 state-listed threatened mussel species currently have no available data

Table 3. The unionids of Texas with no available host species data and their corresponding state and federal listing status.

Species	State Status	Federal Status	Texas Endemic (Y/N)
Fusconaia lananensis	Threatened	Positive 90-day finding; 12-month finding after FY 2016	Y
Obovaria jacksoniana	Threatened	N/A	N
Potamilus amphichaenus	Threatened	Positive 90-day finding; 12-month finding after FY 2016	N
Potamilus metnecktayi	Threatened	Positive 90-day finding; 12-month finding after FY 2016	N
Quadrula apiculata	N/A	N/A	N
Quadrula aurea	Threatened	Candidate*; Proposed rule after FY 2016	Y
Quadrula couchiana	N/A	N/A	N
Quadrula houstonensis	Threatened	Candidate*; Proposed rule after FY 2016	Y
Quadrula mitchelli	Threatened	Positive 90-day finding; 12-month finding after FY 2016	N
Quadrula petrina	Threatened	Candidate*; Proposed rule after FY 2016	Y
Truncilla cognata	Threatened	Positive 90-day finding; 12-month finding after FY 2016	N
Truncilla macrodon	Threatened	Candidate*; Proposed rule after FY 2016	Y
Uniomerus declivis	N/A	N/A	N

Notes: N/A = Not Applicable, no specific listing status; **FY** = Fiscal Year.

* On October 6, 2011, the United States Fish and Wildlife Service (the Service) announced the completion of a status review and determined that the mussel species warranted listing under the Endangered Species Act (ESA).

Explanation for "Positive 90-day finding, and 12-month finding". Section 4(b) of ESA requires the Service to make a finding on whether a petition presents substantial scientific or commercial information to indicate that the petitioned action may be warranted; this is referred to as a 90-day finding. If the Service finds the petitioned action may be warranted, the ESA requires the Service to initiate a formal review to determine if the petitioned action is warranted and, if so, how it intends to proceed with the requested action. This second determination is referred to as a 12-month finding, and is normally made 12-months following the receipt of the petition.

Explanation for "after FY 2016". Depending on the species, the Service will either issue a 12-month finding or develop a proposed rule to list the species. The Service recently created a work plan and entered into two settlement agreements resulting from past lawsuits regarding actions under the listing program nationwide. This work plan focuses on preparing proposed and final rules for listing species that were already candidates (as of December 2010) and outlines the Service's intended listing activities from Fiscal Year (FY) 2011 through FY 2016. Therefore, the earliest the Service expects to begin work on a proposed rule for the central Texas mussels would be in FY 2017 (USFWS 2011a, 2011b).

Qon host species (Table 3). In addition, 12 of the 15 state-listed threatened species have been petitioned for federal listings (USFWS 2014). Six of these 12 species, including *P. popeii*, *Lampsilis bracteata*, *Quadrula aurea*, *Quadrula houstonensis*, *Quadrula petrina*, and *Truncilla macrodon* are currently candidate species for federal protection, and a proposed rule to list or withdraw the species is anticipated after fiscal year 2016 (USFWS 2014). The remaining six mussel species including *Fusconaia lananensis*, *Pleurobema riddellii*, *Potamilus amphichaenus*, *Potamilus metnecktayi*, *Quadrula mitchelli*, and *Truncilla cognata* have had positive 90-day findings and will undergo 12-month status reviews to determine if they warrant federal protection after fiscal year 2016 (USFWS 2014). Of these 12 species petitioned for federal listings, only two species, *P. popeii* and *L. bracteata*, have any host data available (Tables 1, 3).

This literature review on the known and/or potential hosts for the mussels of Texas is intended as a reference tool and foundation for future Texas host research. The threatened status of many Texas mussels at the state level and the potential addition of federal protection in the near future underscore the need for host information, which will greatly enhance the effectiveness of conservation and management of the remaining populations. A management protocol for the joint protection of mussel species and their respective host(s) species will likely be a fundamental component for the successful future conservation of imperiled mussels within Texas.

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