Survey Results and Habitat Use for *Popenaias popeii* (Texas hornshell) in the Rio Grande and Devils River, Texas.

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Executive Summary

The goal of this study was to determine the status, distribution, and mesohabitat associations for *Popenaias popeii* (Texas hornshell), a candidate for protection under the Endangered Species Act, in the upper and middle Rio Grande and the Devils and Pecos Rivers. We compiled all known records of occurrence from published reports and museum records to establish the historical range for this species in Mexico, New Mexico, and Texas. We used recent and historical data to inform a year-long sampling program across the range of *P. popeii* in Texas. In total, we surveyed 114 sites in the Rio Grande and collected 2,063 individuals of *P. popeii* from 29 of the 114 sites surveyed. *Popenaias popeii* was less abundant (n = 189 live individuals) but more prevalent (37% or 14/38 sites) in the upper Rio Grande (n = 189 live individuals) compared to the middle Rio Grande (n = 1,874 live individuals; 20% or 11/74 sites). For the Devils River, we surveyed 11 sites and collected 35 live individuals across two different locations. For the Pecos River, we surveyed 15 sites across three different reaches located near the confluence with Independence Creek, at Pandale Road Crossing, and between Paint Rock Rapids and the weir dam near the reservoir interface with Lake Amistad. A single live individual was found near Pandale, TX, which represents an important find as the last observation of live *P. popeii* in the Pecos was ~ 47 years ago. Results from our Indicator Species Analysis indicate that *P. popeii* primarily occurs in rocky-type habitats (rock slabs, canyon walls with crevices, boulders, and large cobble). Comparing our results to previous studies in the Rio Grande, we found *P. popeii* occupying more sites (i.e., number of sites *P. popeii* was detected) and at higher abundance near Laredo, TX, than previous efforts had suggested. For the Rio Grande near Del Rio and Eagle Pass, TX, we did not find *P. popeii*, which corroborates previous findings in these areas. We also discovered a new population for *P. popeii* upstream from Lake Amistad in the Lower Canyons of the Rio Grande Wild and Scenic River and the Pecos River near Pandale, TX, and confirmed the presence of a population in the Devils River. For the Rio Grande, population size frequency distributions, using shell length as a proxy for age, suggest that recruitment is occurring. We also observed reproductively active females (gravid, i.e., gills containing a brood of either developing eggs or viable larvae) in the upper and lower Rio Grande and Devils River.

Introduction:

Popenaias popeii, Texas hornshell, is known in Texas historically from the Rio Grande and the following tributaries: Pecos River, Devils River, and Las Moras Creek (references in Howells 1999). Type specimens of the species were collected from the Devils River, Val Verde County, Texas by Captain John Pope (~1853) and Rio Salado, Nuevo Leon, Mexico by Jean Louis Berlandier (~1828). Records of questionable validity exist from the Colorado watershed in Central Texas; one specimen from the Llano River collected in 1972 and identified by Stansbery in 1973 (OSUM 1972:365) and one valve from the South Concho River collected in 1991 after a flood (Strenth et al. 2004). These are the only records from central Texas and are likely spurious; either misidentified false spike (*Fusconaia mitchelli*) which tend to be elongated in the upper Colorado basin and look more like Texas hornshell than elsewhere, or misplaced shells from the Rio Grande or Pecos River drainages.

Within the Rio Grande proper, the upstream and downstream limits for *P. popeii* are not well supported. The downstream range limit for *P. popeii* is based on specimens collected by R. D. Camp, a naturalist and purveyor of biological specimens in the early 20th century, and are attributed to the Keller Resaca, an oxbow of the Rio Grande near Brownsville, TX. However, *P. popeii* is not known to occur in lentic habitats such as oxbows as determined by recent sampling (Karateyev et al. 2015), and our own analyses. Camp's collection is currently housed at the Corpus Christi Museum, Corpus Christi, TX, and was inventoried by Raymond Neck, a biologist and malacologist for TPWD, in the early 1980s Neck (1987). In his inventory, Neck provided a list and notes on Camp's molluscan collection, which included comments on the overall condition of the collection and that a number of specimens were either missing or had questionable labels. For the *P. popeii* specimens, Neck (1987) observed calcium carbonate residue on the posterior margin of the specimens, which led him to question whether these specimens actually originated from the Brownsville area. In the Rio Grande, shells that show precipitated calcium carbonate are usually found in spring-fed, hard water, flowing environments like that of the Devils River not slackwater habitats like oxbows. To confirm Neck's (1987) observation, we visited the Corpus Christi Museum in November 2015. During our visit, we found that the identification of these specimens was correct, but the original locality information was missing, and calcium carbonate residue was present on the specimens. Given that the locality for these specimens cannot be confirmed, then the most downstream record of confirmed *P. popeii* in the Lower Rio Grande is at Chapeño, Starr County, TX, which is located immediately downstream of the present Falcon Dam, prior to the dam's completion in 1954 (Neck 1987; Neck and Metcalf 1988). This location is approximately 350 river kilometers upstream of Brownsville. The upstream range limit in the Rio Grande proper prior to data presented herein was thought to be at Bullis Fold (Dean Canyon), downstream of Big Bend National Park in Brewster County where Howells (1999) collected recently and long dead specimens. The most upstream collection of live material prior to our surveys was near Langtry, Val Verde County, Texas (Karatayev et al. 2012).

In tributaries, Texas hornshell is known to have existed in the Devils River from the confluence with the Rio Grande upstream to Finnegan Springs, Val Verde County at present (Strecker 1931, data herein). Las Moras creek from the Rio Grande to the source at Fort Clark Springs, Kinney County (USNM_01 (1898) E. A. Mearns). The Pecos River, from Barstow, TX, Ward County (J.D. Mitchell, ~1890, USNM 464732) to the mouth of the Pecos at the Rio Grande (Metcalf 1974, 1982; A.L. Metcalf 1974, USNM 709228). For Las Moras Creek, live *P. popeii* were collected in 1898 by E. A. Mearns, a physician and naturalist stationed at Fort Clark (USNM 01, 130175,151538, 308943; MCZ 295007). In 1902, the U.S. Army walled in the spring and in 1939 a concrete swimming pool was constructed next to the spring head by the Works Progress Administration (Haen 2002). The springs temporarily ceased to flow in 1964 and 1971 (Brune 1981). From 1971-75, Harold D. Murray, a Professor at Trinity University, surveyed 48 km of Las Moras Creek in search of *P. popeii* but was unable to locate live individuals or shell (Murray 1975). He also observed workers removing heavy plant growth from the creek, which according to local landowners was repeated 2 to 3 times a year starting in 1971 (Murray 1975). It is unknown if this practice continues today. Based on this observation and the lack of live individuals, Murray (1975) argued that *P. popeii* had been extirpated from Las Moras Creek. Portions of Las Moras Creek were informally resurveyed in 1995 by Texas Parks and Wildlife (Howells et al 1997) and Karateyev et al in 2000s. To date, no live or dead *P. popeii* have been collected from Las Moras Creek since Mearns' collections in 1898 (Karatayev et al. 2015).

For reaches of the Pecos that flow through Texas, weathered shell material for *P. popeii* has been collected near Barstow, TX, Ward County (J.D. Mitchell, ~1890, USNM 464732), though Karatayev et al. (2012), Burlakova and Karatayev (2014) and Karatayev et al. (2015) incorrectly reported these individuals as live at time of collection. Downstream of this location, a single fragment of a *P. popeii* shell has been found from the Pecos River near Iraan, TX (Pecos/Crockett Counties) and long dead shells from an ~ 8 km stretch in the lower Pecos, just upstream from the confluence with the Rio Grande. Between these locations, live *P. popeii* have been collected near Pandale, Val Verde County, Texas downstream of the Independence Creek confluence in 1973 (A.L. Metcalf 1974, USNM 709228).

In New Mexico, *P. popeii* was recorded historically from recent shell material on the Pecos River at Carlsbad (R.J. Drake, 1948 USNM 758208) and live individuals were found in its tributary the North Spring Creek near Roswell (Cockerell 1902). The species is only known currently in the Black River near Malaga (Neck 1984; Lang 2001; Strenth et al. 2004; Carman 2007) but long dead shells were found in the Pecos proper downstream from the Black's confluence and in the neighboring Delaware River in the 1990s (Lang 2001). Reintroduction efforts into the Delaware River using adults from the Black River have recently started (2015 Fisheries Management Plan, New Mexico Game and Fish).

The current status of Texas hornshell in Mexico is unknown. Records exist from the Rio Salado watershed which flows into the Rio Grande at Falcon Lake, as well as other drainages to the south that flow to the Gulf of Mexico: the Soto de Marina, Tamesi,

Panuco, Cazones, and Tamul watersheds (Hinkley 1907). However, the genetic identity of the specimens from outside of the Rio Grande watershed have not been confirmed as *P. popeii* and may represent other species, e.g., *Popenaias metallica.*

Until recently Texas hornshell was considered extremely rare. Singley (1893) recorded *P. popeii* from very few locations (in the Devils and Pecos Rivers) and commented that this species was rare. Neck (1982) suggested considering this species for listing by the USFWS. Williams et al. (1993) listed the species as threatened and more recently elevated it to endangered (Williams et al. in review). NatureServe ranks *P. popeii* as critically imperiled across its range and this species is currently listed as a candidate for protection under the U.S. Endangered Species Act (USFWS 2001). Surveys by Miller et al. (unpublished data), Karatayev et al. (2012), and Burlakova and Karatayev (2014) have reported live individuals or recently dead specimens for this species from the Devils River (Val Verde Co.), Rio Grande near John's Marina (Terrell Co.), Del Rio, TX (Val Verde Co.), and Laredo, TX (Webb Co.). These surveys were not initially designed to detect species with low abundance, assess evidence of recruitment, or provide population estimates. Thus, the conservation status of this species throughout the Rio Grande is still uncertain.

Popenaias popeii is considered a valid species (Chapman et al. 2008) and like other freshwater mussels species is an obligate ectoparasite on one or more host-fish species. Reproductive information for this species has been collected from studies focused on a small, disjunct population from the Black River in New Mexico. There, *P. popeii* was considered a short-term brooder, spawning during the early summer months of May and June (Smith et al. 2003). Potential host fishes identified through artificial inoculations in the laboratory include: Longnose gar, Gizzard shad, Mexican tetra, Red shiner, Common carp, Roundnose shiner, Plains minnow, Speckled chub, Rio Grande shiner, Flathead minnow, Central stoneroller, River carpsucker, Blue sucker, Grey Redhorse, Yellow bullhead, Channel catfish, Plains killifish, Rainwater killifish, Western mosquitofish, Rio Grande cichlid, Green sunfish, Bluegill, Longear sunfish, Largemouth bass, and Greenthroat darter (references in Carman 2007). These results suggest that *P. popeii* lacks specialization for attracting specific host species (host generalist – see Barnhart et al. 2008) and employs an opportunistic strategy for host infection, including the free release of glochidia with larval threads that can attach to both skin and gills of hosts (Carman 2007). However, only a small number of these fishes have been observed to harbor parasitic larvae from *P. popeii* in the river (Levine et al. 2012). This indicates that most of the hosts identified during laboratory testing may not be effective hosts for *P. popeii* in the wild. To date, reproductive timing and host-fish relationships for populations in the Rio Grande or Devils River have not been assessed. This information is important for determining which factors (biotic, abiotic, or both) may be responsible for the decline of this species.

Popenaias popeii have been reported to reside in rock crevices, travertine shelves, and under large boulders, where small-grained material, such as clay, silt, or sand gathers (references in Carman 2007; Howells 2010). Karatayev et al. (2012) and Burlakova and Karatayev (2013) performing surveys in portions of the upper and middle Rio Grande

reported similar observations, however, their findings were also anecdotal as they primarily focused on habitats that were known or suspected to harbor *P. popeii* populations (i.e., rock slabs and boulders). Other habitats that may be suitable for mussels (e.g., banks or backwater areas) were not surveyed. Thus, habitat associations for this species remain untested and for juveniles, undescribed.

The objectives of this study were to assess the distribution, abundance, and habitat use for *P. popeii* in the Rio Grande. The resulting survey information was then used to develop Conservation Status Assessment Maps for this species within the Rio Grande and major tributaries.

Methods

Study Area

The Rio Grande originates in Colorado and is considered the 4th largest river in the United States, with an approximate length of 3,050 km and draining a totaling 870,236 km^2 (Kammerer 1990). The river flows from San Juan County, Colorado, through New Mexico and into Texas where it forms the shared border between Texas and Mexico before emptying into to the Gulf of Mexico near Brownsville, TX (Benke and Cushing 2011). Throughout its length the Rio Grande flows through arid and semiarid desert scrubland and grassland habitats (Dahm et al. 2005). Flow in the Rio Grande is regulated by two large reservoirs (Falcon Reservoir and Lake Amistad) and a number of small low-head dams. The World Wildlife Fund currently ranks the Rio Grande as the most imperiled river in the United States due to water over-extraction and over-appropriation by human populations along the river (Wong et al. 2007). The Devils River is a pristine tributary to the Rio Grande originating in Sutton County, TX, and flows intermittently southward into Val Verde County, TX, where it becomes perennial. Flow is unregulated and provided from groundwater seepage and springs. The river lies within the Edwards Plateau region and drains an approximate area of 10,000 km^2, which is sparsely populated (Cantu and Winemiller 1997). The Pecos River flows from the Rocky mountains in north-central New Mexico south to Texas through arid landscapes where much of its water is captured by impoundments for agricultural, municipal, and industrial use. Below Red Bluff Dam near the Texas-New Mexico border the river flows freely, but suffers from elevated salinity levels until receiving groundwater input, most notably at Independence Creek. The river then flows through remote desert before it empties into Amistad Reservoir, where it joins the Rio Grande above Del Rio, Texas.

The present study was located primarily in the upper (upstream of Lake Amistad) and middle (between Lake Amistad and Falcon Reservoir) portions of the Rio Grande in Texas, although several sites were surveyed immediately downstream of Lake Falcon. For the Devils River, sampling was conducted between Baker's Crossing at the Highway 163 bridge and the Big Satan (South) unit of the Devils River State Natural Area (Figure 1). For the Pecos, a reconnaissance sampling trip was performed during March 16 – 21, 2016 near the confluence of Independence Creek, at Pandale Road Crossing, and between Paint Rock Rapids and the weir dam near the reservoir interface with Lake Amistad.

Sampling Methods:

Survey sites within the Rio Grande were selected following methods outlined by Albanese et al. (2007). Specifically, 10-digit HUC watersheds were used to delineate the entire length of Rio Grande within our study area. Species occurrence data from previous sampling efforts in the Rio Grande were then used to determine the following: 1) HUC watersheds where live individuals for *P. popeii* have been reported; 2) HUC watersheds that have been surveyed, but *P. popeii* was not found; and 3) HUC watershed that have not been surveyed. The resulting map was then used to prioritize survey needs by focusing on areas that have not been surveyed (UNS_HUCs) or in areas where past surveys failed to detect *P. popeii* (ND_HUCs). For a subset of HUCs that met these criteria and could be accessed safely using a motorized boat, we delineated the entire length of the river into 10 km reaches. Within each reach specific sites were selected using a random sampling design with 2 strata: river left or river right (except for midchannel habitats) and 2) mesohabitat: (banks, backwater, midchannel, riffles, rock slabs, canyon walls (only for reaches located in the upper Rio Grande), and pools (only for reaches in the Devils River). In total, 10 sites in the middle and 12 sites in the upper Rio Grande, 2 per habitat type, were selected within each reach for sampling. Sites in the Devils River were selected randomly from available mesohabitats, with a focus on deep water habitats that had not been surveyed during previous efforts, and habitats similar to those where *P. popeii* occurs in the Rio Grande. For the Pecos, sites were selected by distance from access point, then by presence of habitat typical of occupancy by Texas hornshell as found in the Rio Grande, Black, and Devils Rivers. Specifically, sites were sampled between ~ 0.1 and 2 km downstream from the confluence of Independence Creek, within ~2 km upstream and ~2 km downstream of the Pandale Road Crossing, and between Paint Rock Rapids and the weir dam near the reservoir interface with Lake Amistad. All sites were 150 m^2 in area and were searched for 4 person-hours visually and tactilely either by snorkel or SCUBA.

Qualitative surveys using the timed search method were performed in each randomly selected mesohabitat type. The timed search method was chosen because it provides a more effective means of detecting rare species than quantitative sampling methodologies (Vaughn et al., 1997). At each site (i.e., mesohabitat type), we confined the search boundaries to the specific habitat type, ensuring that the search area did not exceed 150 m^2. Each site was surveyed tactilely and visually for a total of 4 person-hours (p-h). However, because we are interested in the amount of effort needed to detect *P. popeii* (which will be important for designing long-term monitoring programs), we divided the total search time into 4, 1 p-h intervals. At the end of each search interval, surveyors combined all live specimens into a mesh bag, which was kept submerged in water until completion of the survey. During each interval, surveyors were spread out in the search area and every effort was made to search all available microhabitats. Following completion of the survey, all live mussels from each time period were identified to species, counted, measured, checked for gravidity, and then returned back to the river into the appropriate habitat.

Data analysis:

Bar graphs were used to visually explore relationships between *P. popeii* and total mussel abundance (converted to log scale) and relative abundance (CPUE: number of individuals/total person-hours) by sampling reach. Scatter plots of abundance and relative abundance (CPUE: number of individuals/total person-hours) vs. river kilometer (RKM) were used to examine the effect of stream position on total mussel and *P. popeii* abundance. Boxplots and length-frequency histograms were developed for *P. popeii* to assess demographic patterns and population structuring within populations. Generally, multimodal size class distribution may indicate recruitment, whereas truncated distributions (absence of a particular age class, large, or small individuals) may indicate a lack of recent recruitment or a localized extinction event. For the Pecos population, no analyses were performed because sample size (number of individuals and number of sites) is too small to draw any conclusions.

Indicator Species Analysis (ISA - Dufrêne and Legendre, 1997) was used to test the affinities of *P. popeii* to different habitat types. ISA identifies species or assemblages that are indicative of groups of sites, which have some ecological, conservation or management meaning (Dufrêne and Legendre, 1997). In the present study, we defined groups by mesohabitat type (i.e., riffle, midchannel, pool, backwater, rock slab, and rock face). ISA as proposed by Dufrêne and Legendre (1997) assigns an indicator value (IV) to each taxon by calculating the product of the relative frequency and relative average abundance of each species to a mesohabitat type. The probability of achieving an equal or larger IV value among groups (p) is then estimated based on 999 random permutations of the original data (Dufrêne and Legendre, 1997). ISA was performed with the INDICSPECIES package in R version 3.02 (R Foundation for Statistical Computing, Vienna, Austria), and we considered p-values ≤ 0.10 to be significant.

Conservation maps:

Conservation maps were developed using the Conservation Status Map package provided by the Georgia Department of Natural Resources (http://www.georgiawildlife.com/conservation_status_assessment_maps). Presence/absence data was obtained from the IRNR – Mussel Database, Texas Parks and Wildlife Department [TPWD], Texas Department of Transportation [TxDOT], Texas Commission on Environmental Quality [TCEQ], Texas Water Development Board [TWDB], and published literature. Locality information accompanying each record was georeferenced using ESRI ArcGIS ArcMAP 10.0.

Results/Discussion

A total of 456 person-hours were spent surveying 114 sites located in the Rio Grande (Figure 1). A total of 2,063 live individuals of *P. popeii* were found across 29 sites in the upper (n = 189 individuals) and middle (n = 1,874 individuals) Rio Grande. Total abundance was greatest in Reach 3 (upper Rio Grande, n = 183 individuals), Reach 8 (middle Rio Grande near Colombia, n = 1,155 individuals), and Reach 9 [middle Rio

Grande near La Bota, $n = 652$ individuals] (Figure 2). Relative abundance in the upper and middle portions of the river ranged from 0 to 111 mussels/hr with the highest occurring in Terrell (3 ± 5 mussels/hr; mean ± SD) and Webb (14 ± 27 mussels/ph; mean ± SD) counties (Table 1; Figure 3). These results indicate that *P. popeii* is more abundant in reaches downstream of Lake Amistad. However, the prevalence (i.e., number of sites *P. popeii* was detected) of this species upstream of Lake Amistad was greater (37% or 14/38 sites) than downstream (20% or 15/74), which indicates *P. popeii* may be more widely distributed in the upper Rio Grande. For the Devils River, a total of 44 hrs. across 11 sites was spent searching for mussels. A total of 35 live individuals were collected across 2 of the 11 sites. One site with 34 individuals was located within the Texas Nature Conservancy's (TNC) Dolan Falls Preserve while the site with a singleton was located in the Devils River SNA Big Satan (South) Unit (Table 1). For the Pecos, surveys near Independence Creek yielded no live or dead *P. popeii* from 5 sites. At the reach near Pandale Road Crossing, 1 live and 37 shells were found at 3 of 6 sites. The majority of these (1 live and 28 shells) were found at a single rock wall. At the most downstream reach near the weir dam 46 shells were found from 4 of 4 sites with the majority of shells (27) found in a boulder field approximately 1 m deep.

Prior to this study a significant population of *P. popeii* was known to occur in the Rio Grande immediately upstream of Laredo (Karatayev et al. 2012; Burlakova and Karatayev 2013). Our findings support this observation, but we found *P. popeii* to be more abundant and prevalent within this area than previous efforts had suggested. In the present survey, we examined ~ 40 river kilometers (rkm) spread across 90 rkm between Apache Ranch and La Bota, TX. Within this area, we found a total of 1,874 live individuals (55 ± 108 individuals/site; mean ± SD) across 15 sites or 44% (15/34) of all sites/habitats surveyed. However, for habitats consisting only of rock slabs and boulders, the presumed habitat for *P. popeii*, we collected 1,867 individuals (170 ± 131 individuals/site; mean ± SD) and found this species at 100% (11/11) of those randomly selected sites. In contrast, Karatayev et al. (2012) surveyed ~ 30 rkm between Santa Isabel Creek and the railroad bridge near the Convent Avenue border crossing (located within our study area) and reported 690 live *P. popeii* (12 ± 19 individuals/site; mean ± SD) at 38% (9/24) of all sites surveyed. However, ~ 60% (or 409) of these individuals were from a single mark-recapture site. In a subsequent survey, Burlakova and Karatayev (2013) examining 27 sites (mostly rock-type habitats) across 90 rkm from Apache Ranch to Laredo and documented 334 live individuals (25 ± 84 individual/site; mean ± SD) at 56% (15/27) of all sites surveyed.

For reaches near Del Rio, Eagle Pass, and downstream of Laredo our results corroborate findings by Karatayev et al. (2012) and Burlakova and Karatayev (2013) indicating that *P. popeii* is either extirpated or occurs in extremely low numbers that preclude detection using standard sampling methods.

For the upper Rio Grande, we found *P. popeii* to be more abundant and widely distributed than previously reported. Burlakova and Karatayev (2013) surveying near Langtry, TX, located downstream from our study area, but above Lake Amistad in the Amistad National Recreational Area, found only one live individual. In the upper portion

of our study area in the lower Canyons, between La Linda and El Recodo Canyon, Brewster County (~ 50 rkms), we collected 6 individuals (0.25 ± 0.61; mean ± SD) across 17% (4/24) of the sites surveyed, which indicates that this stretch of the lower Canyons likely represents the upper distribution limit for *P. popeii* in the lower Canyons and mostly likely the Rio Grande (Figure 7). Downstream from the upper reach, between Bone Watering [Paso Colorado Crossing] and Sanderson Canyon Crossing, Terrell County (~ 13 rkms), we found 149 individuals (30 ± 30; mean ± SD) across 80% (4/5) of the sites surveyed, which represents a hotspot of *P. popeii* abundance in the lower Canyons. Finally, in the most downstream surveyed reach of the lower Canyons, between John's Marina and Arroyo El Zacate, Terrell County (~ 7 rkms), we found 34 individuals (4 ± 7; mean ± SD) across 67% (6/9) of the sites surveyed. The reduction in abundance, compared to the middle reach, indicates that this section of the lower Canyons is not a hotspot of *P. popeii* abundance. However, the fact that this species is present at a majority of rock-type habitats surveyed indicates this reach is likely not the lower end of *P. popeii's* range within the lower Canyons. Similar to reaches near Laredo, TX, rocky-type habitats were the most productive for this species; a total of 183 (11 ± 21; mean ± SD) individuals were collected across 63% (10/16) of sites consisting of rock slabs and boulders as the dominant substrate type.

For the Devils River, previous surveys reported a total of 11 individuals over a 12-year period (Burlakova and Karatayev, 2014) and most of these accounts were from downstream of Baker's Crossing to the Devils River SNA (North unit; above Dolan Falls) and one within the Devils River SNA (South unit; below Dolan Falls). Recent surveys by TPWD biologists in 2014 found a total of 13 live individuals across two sites within the TNC Dolan Falls Preserve. In the present study, we observed 35 individuals across two sites (a total of 11 sites were surveyed), which represents the largest number of live *P. popeii* collected to date from the Devils River. Our results combined with those from recent surveys by TPWD indicate that *P. popeii* may be more abundant in the Devils River than previous efforts have suggested.

For the Pecos River, previous researchers considered *P. popeii* to have been extirpated from this river (Burlakova and Karatayev 2013). The collection of a single live individual near Pandale, TX, plus shell indicates this species continues to persist in the lower Pecos. However, further sampling is needed to determine the exact distribution, abundance, and habitat associations of *P. popeii* in the lower Pecos River.

In the Rio Grande, *P. popeii* was the dominant species when present (Figure 2) and was occasionally found with *Cyrtonaias tampicoensis* (Tampico pearlymussel), *Lampsilis teres* (yellow sandshell), *Megalonaias nervosa* (washboard), *Potamilus metnecktayi* (Salina mucket), *Quadrula apiculata* (southern mapleleaf), *Truncilla cognata* (Mexican fawnsfoot), and *Utterbackia imbecillis* (paper pondshell). In the Devils River, *P. popeii* was the only mussel species collected, though specimens resembling *Potamilus purpuratus* (bleufer) have been found live in the lower reaches of the Devils River SNA. Similar to the Devils River, *P. popeii* was the only species collected in the Pecos, though shell for *C. tampicoensis* was collected near the confluence of Independence Creek.

In the upper and middle Rio Grande, adult and juvenile *P. popeii* were primarily found in rocky-type habitats containing large rocks, boulders, or in crevices along canyon walls (Figure 4), but in the Devils River live individuals were found at the heads of riffles and rapids or in clean-swept pools with bedrock (Figure 4). Indicator species analysis for *P. popeii* from the upper and middle portions of the Rio Grande supported our observation that this species primarily occurs in rocky-type habitats (which includes rock slabs, boulders, crevices along canyon walls) and the results were significant (IV = 0.70, *P*-value = 0.0003). This finding supports observations reported by Carman (2007), Howells (2010) and Karatayev et al. (2012), Burlakova and Karatayev (2014). These results also indicate that the absence of this species from reaches in Del Rio, Eagle Pass, and downstream of Laredo is not the result of sampling bias (i.e., surveyors not examining the correct habitat) as rock slabs and boulders, which are known to support this species in Laredo, John's Marina, and Black Gap WMA, were present and sampled in these reaches. Habitat associations for *P. popeii* from the Devils and Pecos were not tested because our sample size was too small (i.e., number of individuals collected and number of sites surveyed).

Size frequency distributions for the three populations were similar. Median shell length for populations in the upper and middle Rio Grande and Devils River was approximately 71 mm and the minimum and maximum shell lengths were 9.8 mm, 20.8 mm, 45 mm and 104.6 mm, 91.0 mm, and 84.5 mm, respectively (Figure 5). The shape of shell length distributions for all three populations resembles an "inverted teardrop" (*sensu* Miller and Payne 1993), which can be indicative of consistent annual recruitment (Figure 8). It is important to note that for the population upstream of Lake Amistad there appears to be a second mode around 35 mm, which may indicate recent recruitment. However, these results should be viewed with caution as *P. popeii* occupies a unique habitat type (under rock slabs and within rock crevices) that may preclude consistent detection of small individuals. That said, subadults (< 30 mm) were found at 12 of the 31 sites containing *P. popeii*. Three of these sites were from the lower Canyons and the remainder was from upstream of Laredo, TX. Generally, the population upstream of Laredo, TX, appears to have a greater abundance of subadults than the populations in the Lower Canyons or in the Devils River. The largest individuals occur in the upstream population, with several individuals exceeding 100 mm in shell length (Figure 6).

During the course of this study, we observed reproductively active females (gravid, i.e., gills containing a brood of either developing eggs or viable larvae) during summer and fall sampling events that coincide with the reproductive season of that in Black River population (Smith 2003). Specifically, we observed gravid individuals on April 7, 2015 at La Bota, on May 14-15, 2015 at John's Marina, and at Columbia, John's Marina, and La Bota on September 5-8, 2015. The smallest gravid individual observed was 38 mm long, suggesting early sexual maturation. During the September 5-8, 2015 sampling trip, 355 of 904 (39%) mussels observed were gravid. For the Devils River, gravid individuals were collected on September 17, 2015 and only 5 of 34 (15%) were gravid, but sample size was small. These results suggest that timing of spawning in the Devils River may not match that in the Rio Grande populations, which is not unexpected given the cooler water temperatures in the Devils River. Generally, cooler water temperatures

may slow the maturation of fertilized eggs in the marsupium, which can reduce or postpone the period of host infection (Heinricher and Layzer, 1999). The occurrence of gravid females at La Bota in early April, John's Marina in mid-May, and both reaches again in early September suggests that *P. popeii* broods mature larvae for an extended period during summer months, that there may be asynchrony in spawning events within the population, or multiple broods are produced seasonally. The latter has been documented for members of Lampsilini (Parker et al, 1994) and Pleurobemini (Price and Eads, 2011) occurring on the coastal plain. An extended brooding period is likely, but unusual in that *Popenaias* has the ability to utilize many host species (Levine et al 2012), whereas most other "long term brooders" have specialized mechanism to attract a specific host.

Conservation maps populated with presence/absence records from 2000 to present show that recent accounts of *P. popeii* are within the last 5 years, presumably the result of increased sampling effort by qualified surveyors in the Rio Grande. The maps also show that the spatial extent of *P. popeii's* distribution has increased over the last 5 years (Figures 7 & 8). Presence records for *P. popeii* from the past 20 years show that there are 4 disjunct populations within the Rio Grande and tributaries within the United States. Amistad Reservoir is a physical barrier between these populations, and thus preventing gene flow by impeding the movement of fishes bearing *P. popeii* glochidia. Based on the total number of presence records for *P. popeii* within the last 20 years it appears the population just upstream of Laredo, TX, is the largest, but populations in the Lower Canyons and Devils and Pecos Rivers are recent discoveries and located in remote areas and as such have not been sampled as extensively as the Laredo population (Figure 9).

In summary, our results indicate that there are two disjunct populations for *P. popeii* in the Rio Grande: one in the Lower Canyons of the Rio Grande Wild and Scenic River, and the second upstream from Laredo (Figures 2 & 3). Our results also indicate that a third population does occur in the Devils River and a fourth in the Pecos River, but the status of both are still uncertain because overall sampling effort within either river remains limited and lacks sufficient spatial scale to characterize trends and identify environmental factors responsible for patterns in mussel assemblage structure. To date, the Rio Grande downstream of Falcon remains largely unsurveyed due to safety concerns stemming from drug cartel activity. In the present study, several sites were examined downstream of Falcon Lake and live unionid mussels were found, but none were *P. popeii*. Unfortunately, sampling in this portion of the Rio Grande was prematurely suspended after survey crews were temporarily detained by the Mexican Army. In general, habitat immediately downstream of Falcon Lake appears degraded, which is likely the result of frequent impoundment releases (i.e., pulsing) to support hydropower operations. Since dam-induced impacts attenuate with distance from the point of impact it is likely that instream habitat may improve further downstream. However, there are several large urban centers located along the river that discharge effluent of varying levels of pre-release treatment, which may offset any improvements to habitat associated with increased distance from Falcon Lake by degrading water quality.

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Table 1. Locality and collection information for survey sites on the Rio Grande and Devils and Pecos Rivers. Habitat abbreviations correspond to the following: BH – banks; BW – backwater; MC – midchannel; R – riffles; RS – rock slabs; and RW – canyon walls (only for reaches located in the upper Rio Grande). Reach number and corresponding locality are depicted in Figure 1. For the Pecos, the reach abbreviations correspond to the following: ICP = confluence of Independence Creek; PDL = Pandale Bridge Crossing; and WER = Weir). CPUE = mussel abundance per site divided by 4 person-hours. Subadult mussels are defined as individuals that were less than 30 mm in shell length.

Site	Habitat	Reach	Locality	County	Date of collection	Number of live	CPUE	Sub Adult	Effort (hrs)	Area (m^2)
1	MC	1	La Linda	Brewster	6/8/15	0	0	-	4	150
2	BW	1	La Linda	Brewster	6/8/15	0	0	-	4	150
3	RW	1	La Linda	Brewster	6/8/15	0	0	-	4	150
4	BH	1	La Linda	Brewster	6/8/15	0	0	-	4	150
5	R	1	La Linda	Brewster	6/8/15	0	0	-	4	150
6	RS	1	La Linda	Brewster	6/8/15	0	0	-	4	150
7	BW	1	La Linda	Brewster	6/9/15	0	0	-	4	150
8	BH	1	La Linda	Brewster	6/9/15	0	0	-	4	150
9	R	1	La Linda	Brewster	6/9/15	0	0	-	4	150
10	RW	1	La Linda	Brewster	6/9/15	0	0	-	4	150
11	MC	1	La Linda	Brewster	6/9/15	0	0	-	4	150
12	RS	1	La Linda	Brewster	6/9/15	0	0	-	4	150
13	R	2	Black Gap	Brewster	6/11/15	0	0	-	4	150
14	RW	2	Black Gap	Brewster	6/11/15	1	0.25	N	4	150
15	RW	2	Black Gap	Brewster	6/11/15	0	0	-	4	150
16	BW	2	Black Gap	Brewster	6/11/15	0	0	-	4	150
17	RS	2	Black Gap	Brewster	6/11/15	0	0	-	4	150
18	MC	2	Black Gap	Brewster	6/11/15	0	0	-	4	150
19	R	2	Black Gap	Brewster	6/11/15	0	0	-	4	150
20	BH	2	Black Gap	Brewster	6/10/15	0	0	-	4	150
21	BH	2	Black Gap	Brewster	6/10/15	1	0.25	N	4	150
22	RW	2	Black Gap	Brewster	6/10/15	2	0.50	N	4	150
23	RS	2	Black Gap	Brewster	6/10/15	2	0.50	N	4	150
24	BW	2	Black Gap	Brewster	6/10/15	0	0	-	4	150
114	RW	3	John's Marina	Terrell	9/8/2015	47	11.75	N	4	150
25	RW	3	John's Marina	Terrell	5/16/15	72	18.00	Y	4	150
113	RS	3	John's Marina	Terrell	9/8/2015	4	1.00	N	4	150
26	BH	3	John's Marina	Terrell	5/16/15	0	0	-	4	150
27	RW	3	John's Marina	Terrell	5/16/15	26	6.50	Y	4	150
28	BW	3	John's Marina	Terrell	5/14/15	2	0.50	N	4	150
29	RW	3	John's Marina	Terrell	5/14/15	22	5.50	N	4	150
30	R	3	John's Marina	Terrell	5/14/15	0	0	-	4	150
31	BH	3	John's Marina	Terrell	5/15/15	1	0.25	N	4	150
32	BW	3	John's Marina	Terrell	5/15/15	0	0	-	4	150
33	R	3	John's Marina	Terrell	5/14/15	2	0.50	Y	4	150
34	BH	3	John's Marina	Terrell	5/14/15	0	0	-	4	150
35	RW	3	John's Marina	Terrell	5/15/15	5	1.25	N	4	150
36	RS	3	John's Marina	Terrell	5/15/15	2	0.50	N	4	150
37	RS	4	Del Rio	Val Verde	5/13/15	0	0	-	4	150
38	BW	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150
39	BH	4	Del Rio	Val Verde	5/13/15	0	0	-	4	150
40	R	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150
41	BW	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150

Table 1. Continued.

Site	Habitat	Reach	Locality	County	Date of collection	Number of live	CPUE	Sub Adult	Effort (hrs)	Area (m^2)
42	R	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150
43	MC	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150
44	BH	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150
45	RS	4	Del Rio	Val Verde	5/12/15	0	0	-	4	150
46	RS	5	Eagle Pass	Maverick	4/10/15	0	0	-	4	150
47	BH	5	Eagle Pass	Maverick	4/11/15	0	0	-	4	150
48	MC	5	Eagle Pass	Maverick	4/10/15	0	0	-	4	150
49	R	5	Eagle Pass	Maverick	4/10/15	0	0	-	4	150
50	BW	5	Eagle Pass	Maverick	4/11/15	0	0	-	4	150
51	BW	5	Eagle Pass	Maverick	4/11/15	0	0	-	4	150
52	R	5	Eagle Pass	Maverick	4/10/15	0	0	-	4	150
53	MC	5	Eagle Pass	Maverick	5/11/15	0	0	-	4	150
54	BH	5	Eagle Pass	Maverick	5/11/15	0	0	-	4	150
55	RS	5	Eagle Pass	Maverick	4/10/15	0	0	-	4	150
56	R	6	El Indio	Maverick	4/9/15	0	0	-	4	150
57	BW	6	El Indio	Maverick	4/9/15	0	0	-	4	150
58	MC	6	El Indio	Maverick	4/9/15	0	0	-	4	150
59	BW	6	El Indio	Maverick	4/9/15	0	0	-	4	150
60	RS	6	El Indio	Maverick	4/9/15	0	0	-	4	150
61	MC	6	El Indio	Maverick	4/9/15	0	0	-	4	150
62	BH	6	El Indio	Maverick	4/9/15	0	0	-	4	150
63	BH	6	El Indio	Maverick	4/8/15	0	0	-	4	150
64	RS	6	El Indio	Maverick	4/8/15	0	0	-	4	150
65	R	6	El Indio	Maverick	4/8/15	0	0	-	4	150
66	R	7	Apache	Webb	2/24/15	0	0	-	4	150
67	RS	7	Apache	Webb	2/25/15	27	6.75	Y	4	150
68	R	7	Apache	Webb	2/24/15	0	0	-	4	150
69	BW	7	Apache	Webb	2/25/15	0	0	-	4	150
70	BW	7	Apache	Webb	2/25/15	0	0	-	4	150
71	RS	7	Apache	Webb	2/24/15	40	10	Y	4	150
72	BW	8	Columbia	Webb	2/20/15	0	0	-	4	150
73	RS	8	Columbia	Webb	2/19/15	269	67.25	Y	4	150
74	MC	8	Columbia	Webb	2/20/15	0	0	-	4	150
75	R	8	Columbia	Webb	2/19/15	0	0	-	4	150
76	BH	8	Columbia	Webb	2/20/15	0	0	-	4	150
112	RS	8	Columbia	Webb	9/6/2015	444	111.00	N	4	150
77	RS	8	Columbia	Webb	2/20/15	215	53.75	Y	4	150
78	BW	8	Columbia	Webb	11/20/14	0	0	-	4	150
79	R	8	Columbia	Webb	2/19/15	0	0	-	4	150
111	RS	8	Columbia	Webb	9/6/2015	225	56.25	N	4	150
80	BH	8	Columbia	Webb	11/20/14	2	0.50	Y	4	150
81	RS	9	La Bota	Webb	2/21/15	28	7.00	N	4	150
82	BH	9	La Bota	Webb	11/18/14	0	0	-	4	150

Table 1. Continued.

Site	Habitat	Reach	Locality	County	Date of collection	Number of live	CPUE	Sub Adult	Effort (hrs)	Area (m^2)
83	R	9	La Bota	Webb	2/22/15	3	0.75	Y	4	150
84	MC	9	La Bota	Webb	2/21/15	0	0	-	4	150
85	BW	9	La Bota	Webb	11/16/14	0	0	-	4	150
86	MC	9	La Bota	Webb	2/22/15	0	0	-	4	150
87	R	9	La Bota	Webb	2/21/15	1	0.25	N	4	150
88	BW	9	La Bota	Webb	2/22/15	0	0	-	4	150
89	BH	9	La Bota	Webb	11/16/14	0	0	-	4	150
90	RS	9	La Bota	Webb	2/22/15	224	56.00	Y	4	150
91	BW	9	La Bota	Webb	11/18/14	0	0	-	4	150
109	RS	9	La Bota	Webb	9/5/2015	27	6.75	N	4	150
110	RS	9	La Bota	Webb	9/5/2015	184	46.00	Y	4	150
92	R	9	La Bota	Webb	4/7/15	0	0	-	4	150
93	RS	9	La Bota	Webb	4/7/15	184	46.00	Y	4	150
94	BW	9	La Bota	Webb	4/7/15	1	0.25	N	4	150
95	R	9	La Bota	Webb	4/7/15	0	0	-	4	150
96	RS	10	San Ygnacio	Zapata	2/26/15	0	0	-	4	150
97	BH	10	San Ygnacio	Zapata	11/14/14	0	0	-	4	150
98	BW	10	San Ygnacio	Zapata	11/13/14	0	0	-	4	150
99	R	10	San Ygnacio	Zapata	2/18/15	0	0	-	4	150
100	R	10	San Ygnacio	Zapata	2/18/15	0	0	-	4	150
101	RS	10	San Ygnacio	Zapata	2/18/15	0	0	-	4	150
102	MC	10	San Ygnacio	Zapata	11/15/14	0	0	-	4	150
103	RS	10	San Ygnacio	Zapata	2/18/15	0	0	-	4	150
104	MC	10	San Ygnacio	Zapata	11/15/14	0	0	-	4	150
105	BH	10	San Ygnacio	Zapata	11/13/14	0	0	-	4	150
106	BW	10	San Ygnacio	Zapata	2/26/15	0	0	-	4	150
107	BH	11	Salenino	Starr	11/19/14	0	0	-	4	150
108	BW	11	Salenino	Starr	11/19/14	0	0	-	4	150
115	Pool	-	Devils	Val Verde	9/15/15	0	0	-	4	150
116	Pool	-	Devils	Val Verde	9/15/15	0	0	-	4	150
117	MC	-	Devils	Val Verde	9/15/15	0	0	-	4	150
118	Pool	-	Devils	Val Verde	9/16/15	0	0	-	4	150
119	MC	-	Devils	Val Verde	9/16/15	0	0	-	4	150
120	RS	-	Devils	Val Verde	9/17/15	0	0	-	4	150
121	BW	-	Devils	Val Verde	9/17/15	0	0	-	4	100
122	R	-	Devils	Val Verde	9/17/15	34	8.50	N	4	150
123	MC	-	Devils	Val Verde	9/17/15	0	0	-	4	150
124	BH	-	Devils	Val Verde	9/18/15	0	0	-	4	150
125	BW	-	Devils	Val Verde	9/18/15	1	0.25	N	4	150
126	RS	ICP	Pecos	Terrell	3/17/2016	0	0	-	4	150
127	R	ICP	Pecos	Terrell	3/17/2016	0	0	-	4	150
128	P	ICP	Pecos	Terrell	3/17/2016	0	0	-	4	150
129	BH	ICP	Pecos	Terrell	3/17/2016	0	0	-	4	150
130	R	ICP	Pecos	Terrell	3/17/2016	0	0	-	4	150
131	R	PDL	Pecos	Val Verde	3/18/2016	0	0	-	4	150
132	RS	PDL	Pecos	Val Verde	3/18/2016	0	0	-	4	150
133	RS	PDL	Pecos	Val Verde	3/18/2016	0	0	-	4	150
134	RS	PDL	Pecos	Val Verde	3/19/2016	1	0.25	N	4	150
135	R	PDL	Pecos	Val Verde	3/19/2016	0	0	-	4	150
136	BH	PDL	Pecos	Val Verde	3/19/2016	0	0	-	4	150

Table 1. Continued.

Site	Habitat	Reach	Locality	County	Date of collection	Number of live	CPUE	Sub Adult	Effort (hrs)	Area (m^2)
137	RS	WER	Pecos	Val Verde	3/20/2016	0	0	-	4	150
138	RS	WER	Pecos	Val Verde	3/21/2016	0	0	-	4	150
139	RS	WER	Pecos	Val Verde	3/20/2016	0	0	-	4	150
140	RS	WER	Pecos	Val Verde	3/21/2016	0	0	-	4	150

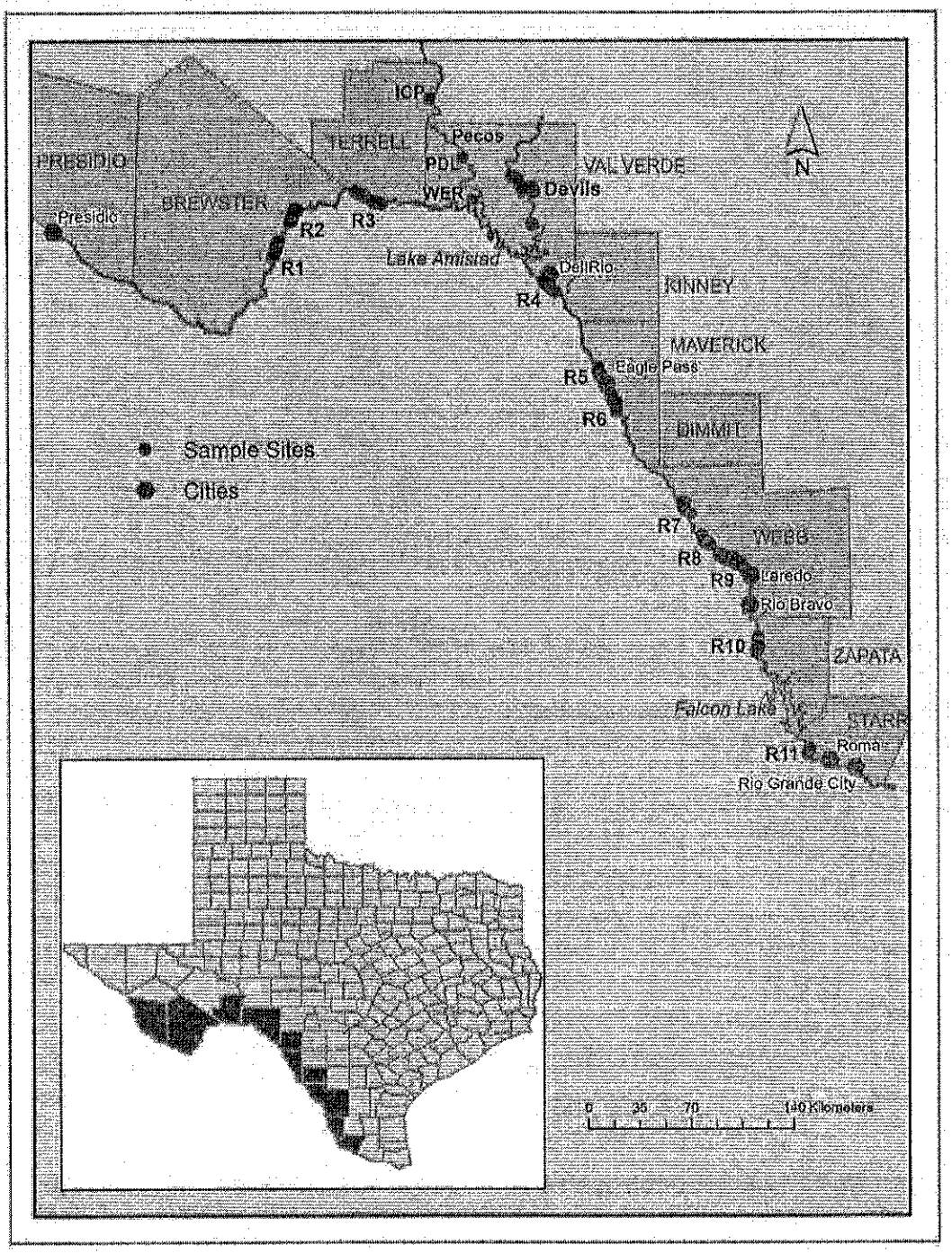

Figure 1. Map of study area. Shaded circles denote sampling locations and letters with numerals indicate sampling reaches.

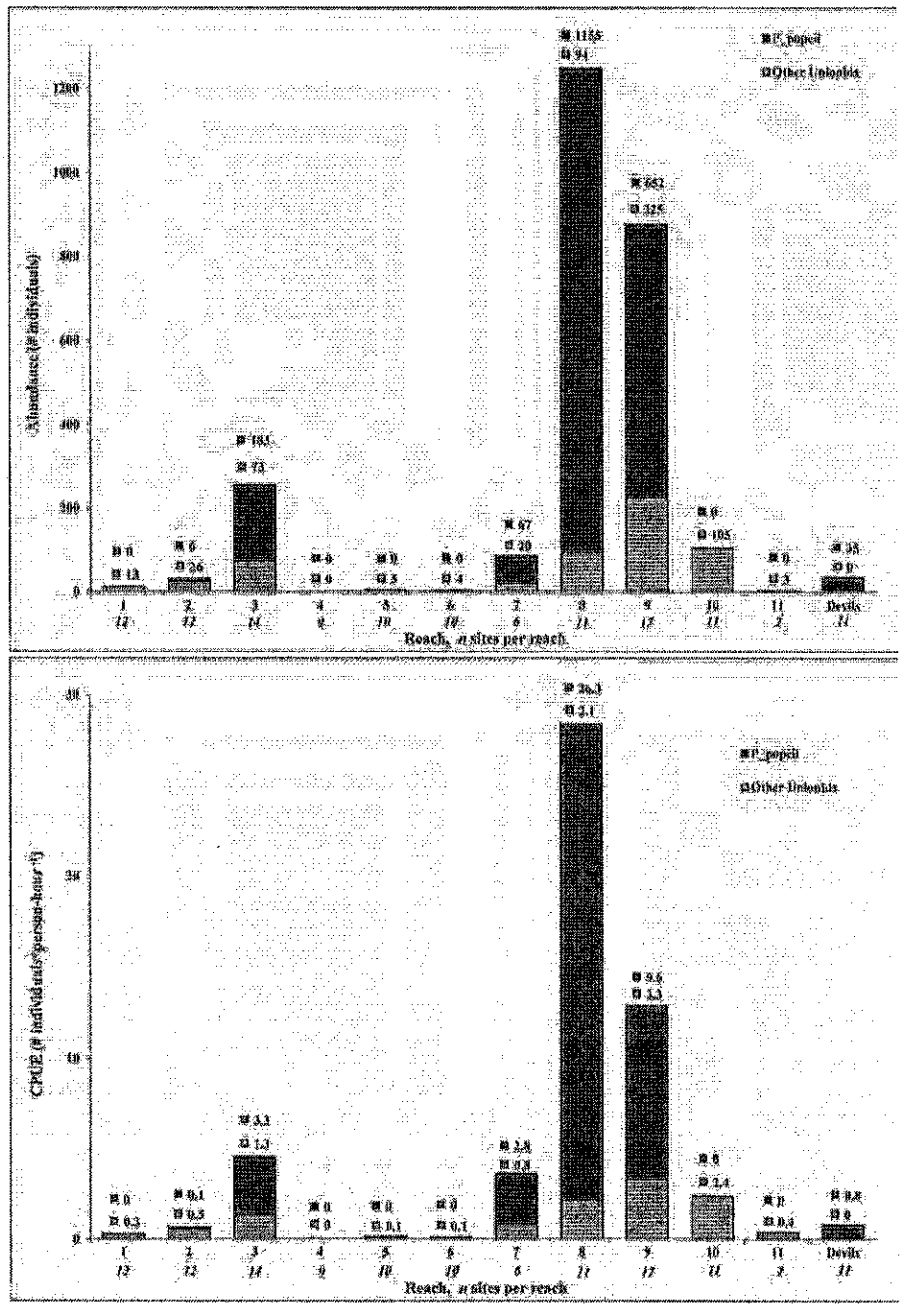

Figure 2. Total abundance (top) and relative abundance (bottom) by reach for all other mussels, "Other Unionids," and *Popenaias popeii* (Texas hornshell), "P_popeii," (see Table 1 for codes). Labels above bars denote total (top) or relative (bottom) number of live individuals collected. CPUE = mussel abundance per site divided by 4 person-hours, as effort was standardized at all sites. The CPUE numbers in this figure represent the totality of abundance divided by the totality of effort expended in each reach. The number of sites per reach determines the amount of effort expended per reach. The Pecos River population is not included in either graph because sample size (number of individuals and number of sites) is too small to draw any conclusions.

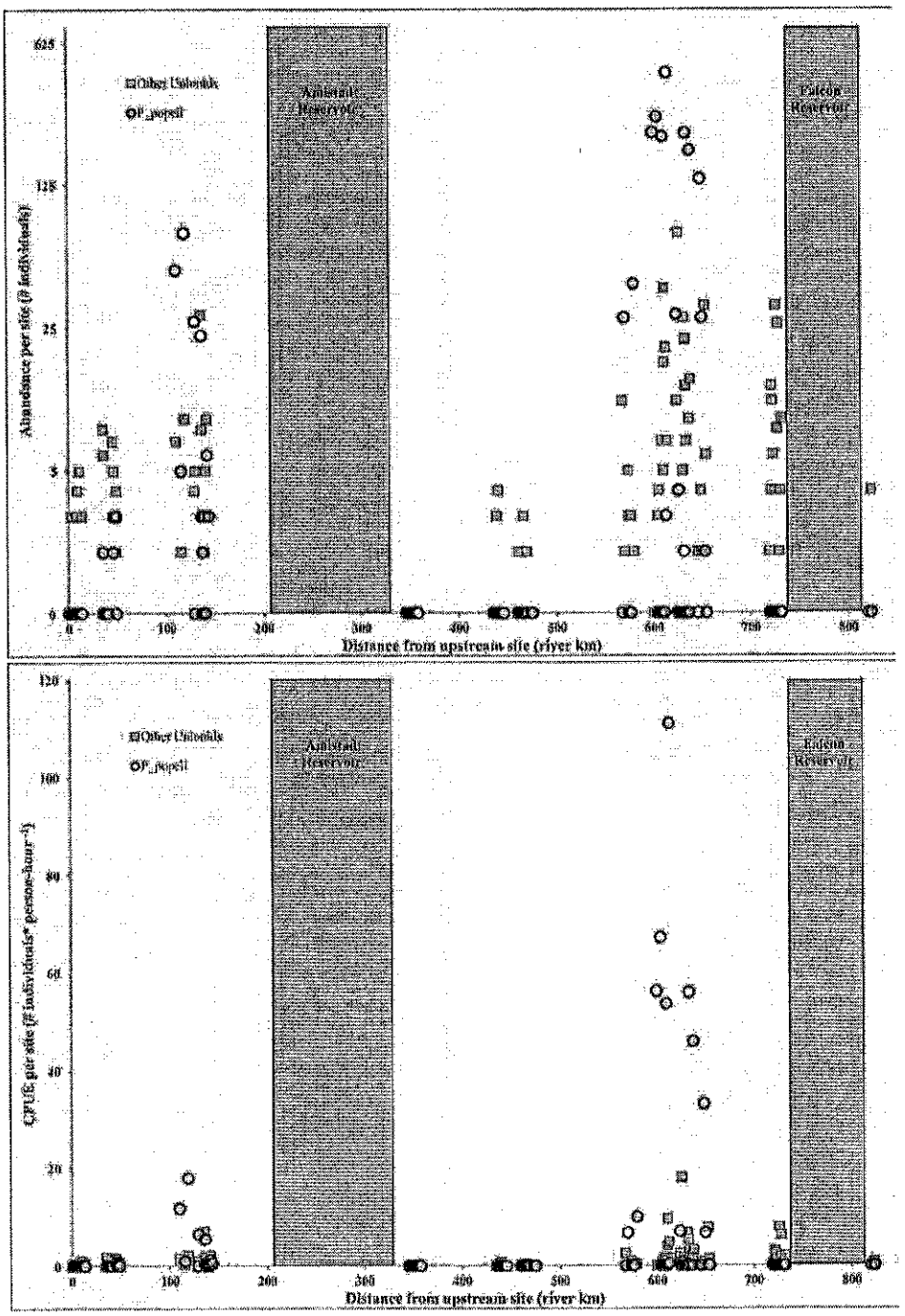

Figure 3. Longitudinal distribution of raw abundance (top) and relative abundance data (bottom) for all other mussel species, "Other Unionids," and *Popenaias popeii* (Texas hornshell), from La Linda to Saleniño, TX. The vertical axis in the top graph is transformed to logarithmic scale (base 5) to display low abundances more clearly. Each point represents species at one sample site. CPUE = total number of either TX hornshell or all other mussels encountered at each site divided by the number of person hours (4) searched at each site.

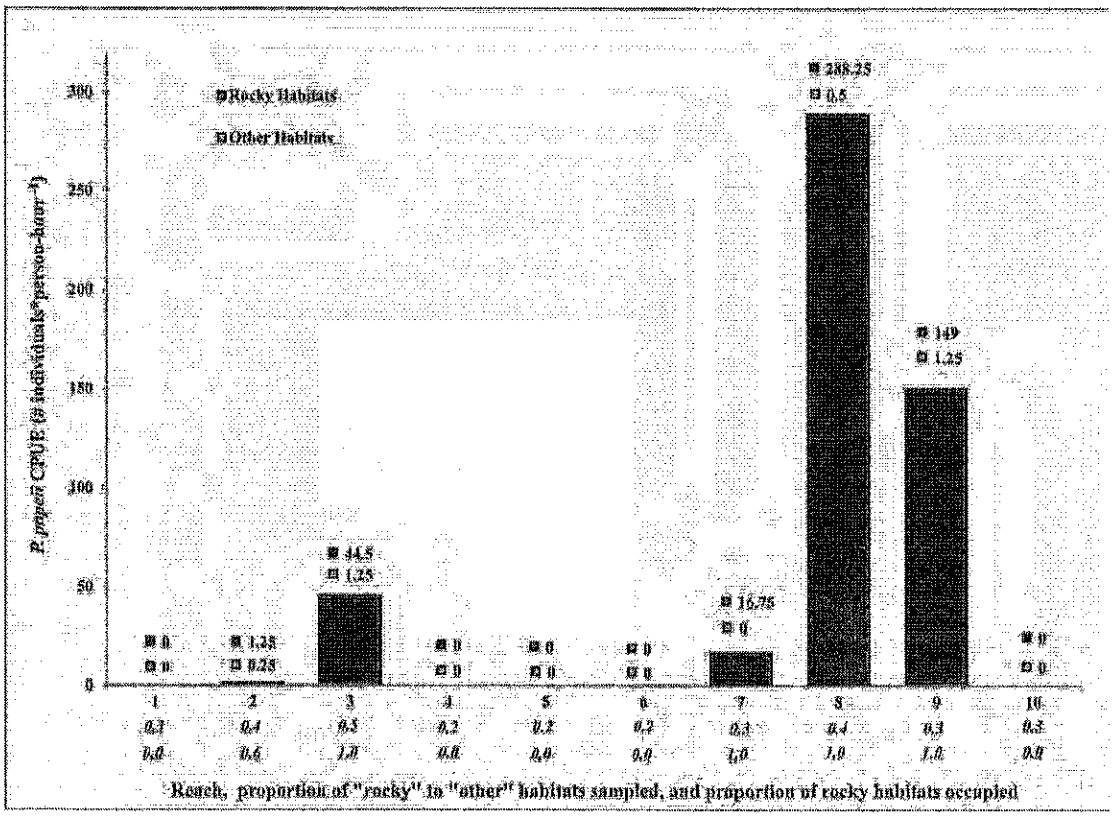

Figure 4. Relative abundance of Texas hornshell at "Rocky" habitats and all other habitat types. Values above bars denote CPUE (i.e., relative abundance) per habitat grouping. The proportion of rocky habitat to other habitat types sampled per reach and presence/absence of Texas hornshell at rocky-type habitats in each reach are listed below the x-axis. CPUE = Texas hornshell abundance per "rocky" or "other" habitat type and represents the totality of abundance divided by the totality of effort expend for each grouping. Note that Reach 11 and the Devils and Pecos Rivers have not been included because sample sizes (i.e., number of sites surveyed) for each are too small to draw meaningful conclusions regarding *P. popeii* habitat associations.

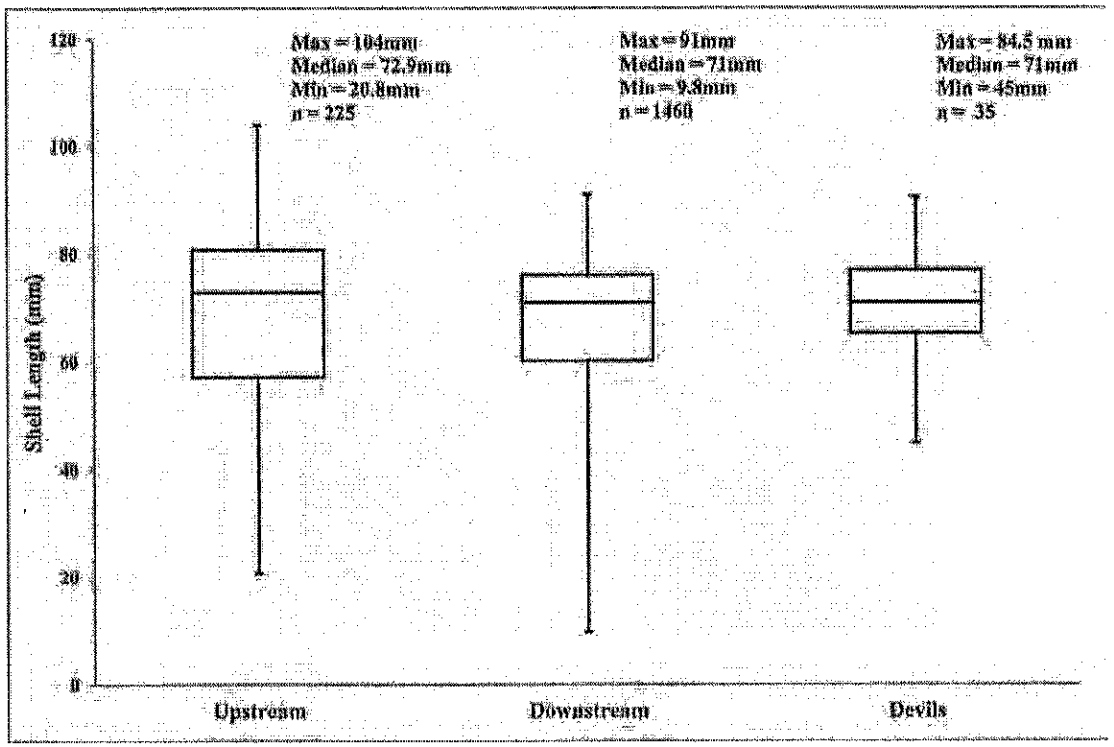

Figure 5. Box and whisker plot of shell length data for *Popenaias popeii* (Texas hornshell) populations from the Rio Grande and Devils River. Labeling on the x-axis denotes the following: "Upstream," represents the population located upstream of Lake Amistad between Black WMA and John's Marina, "Downstream," represents the population from Apache Ranch to Laredo, TX, and "Devils," describes the population between Baker's Crossing at the Highway 163 bridge and the Big Satan unit of the Devils River State Natural Area. The Pecos River population is not included because sample size (number of individuals and number of sites) is too small to draw any conclusions.

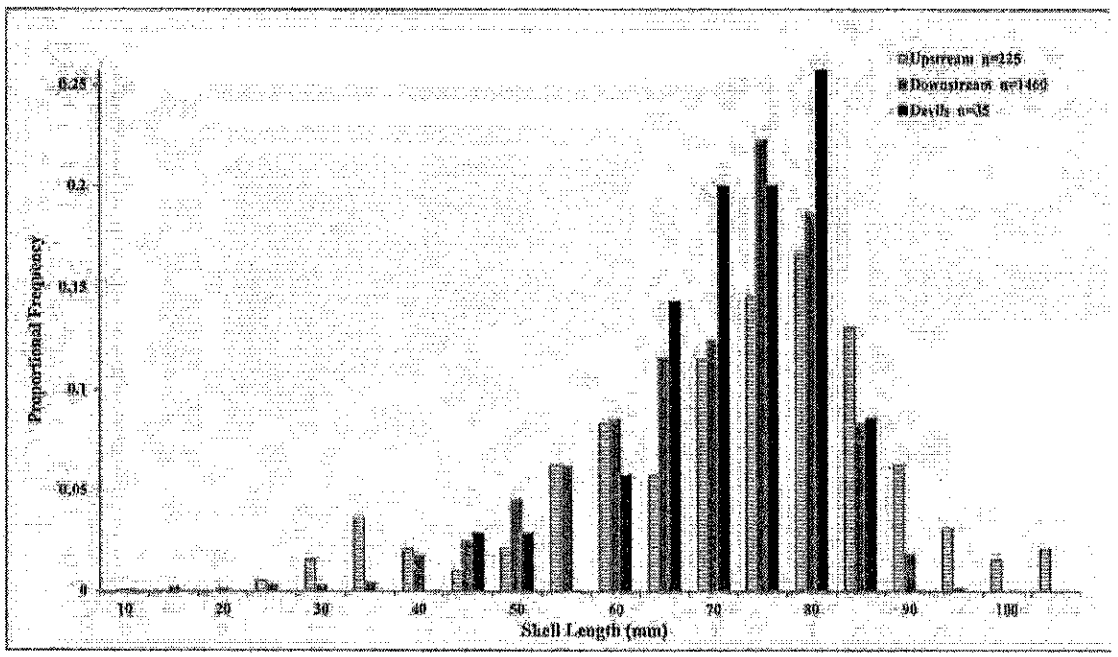

Figure 6. Proportional frequency of shell lengths for *Popenaias popeii* (Texas hornshell) from the Rio Grande and Devils River. The "Upstream" population is located in the Rio Grande upstream of Lake Amistad between Black WMA and John's Marina, the "Downstream" population is located in the Rio Grande and ranges from Apache Ranch to Laredo, TX, and the "Devils River" population is located between Baker's Crossing at the Highway 163 bridge and the Big Satan unit of the Devils River State Natural Area. Shell lengths are binned into 5 mm groups. The Pecos River population is not included in because sample size (number of individuals and number of sites) is too small to draw any conclusions.

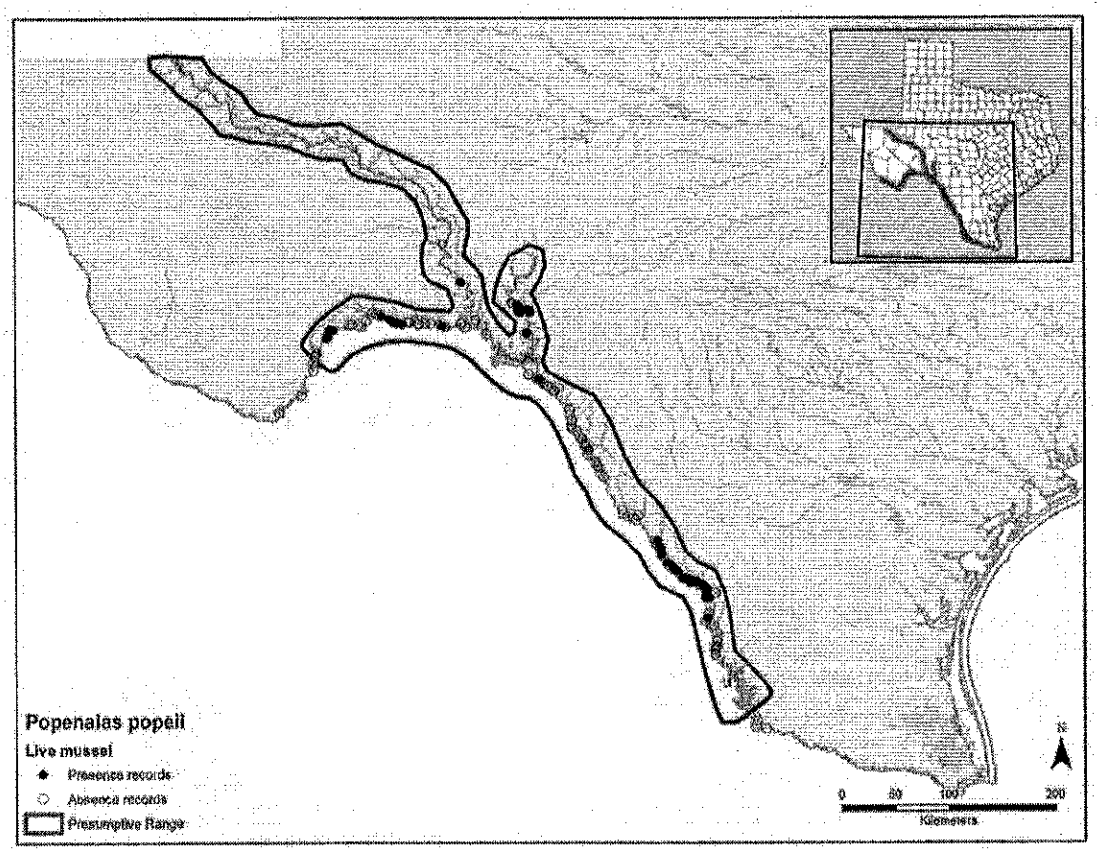

Figure 7. Map of survey locations in the Rio Grande. Shaded circles denote presence and unshaded circles indicate absence for *Popenaias popeii* (Texas hornshell). Survey sites shown are from 2000 to present and are taken from the present study plus those obtained from academic, state, and federal agencies.

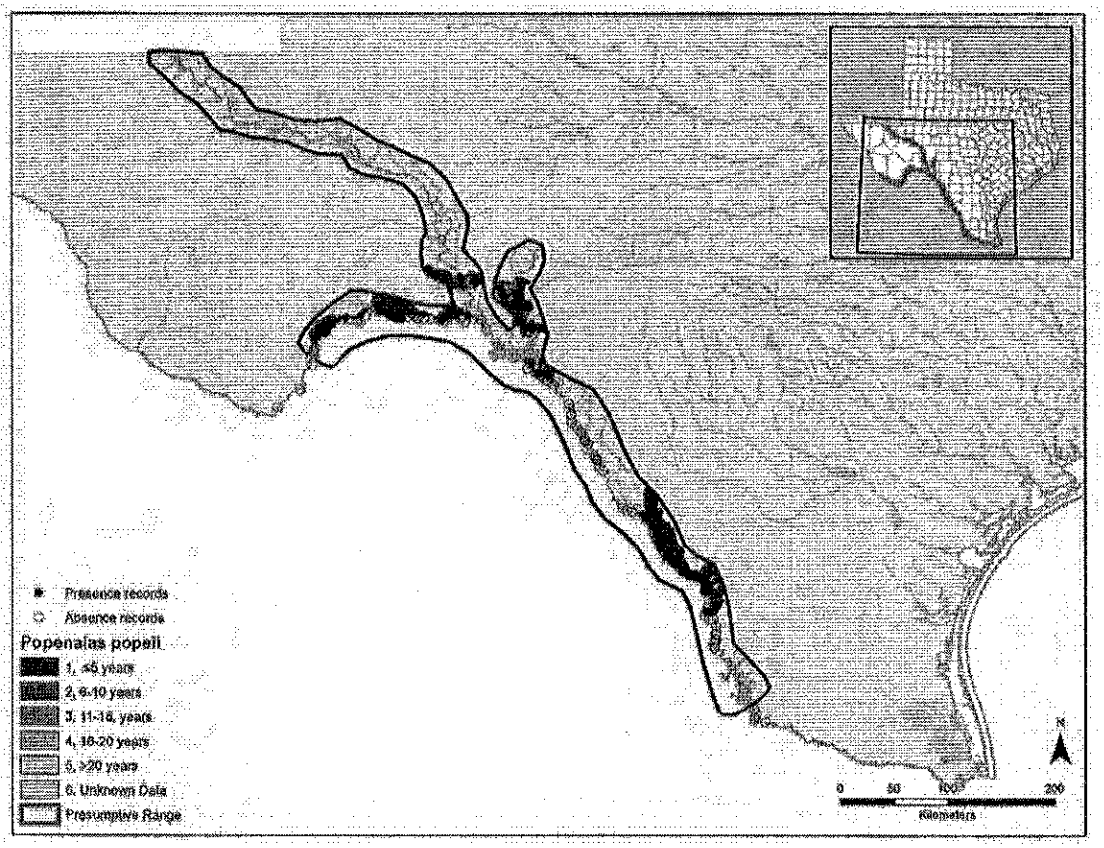

Figure 8. Conservation assessment map for *Popenaias popeii* (Texas hornshell). Shaded circles denote presence and unshaded circles indicate absence for *P. popeii*. Survey sites shown are from 2000 to present and are taken from the present study plus those obtained from academic, state, and federal agencies. HUCs are colored based on date of sampling.

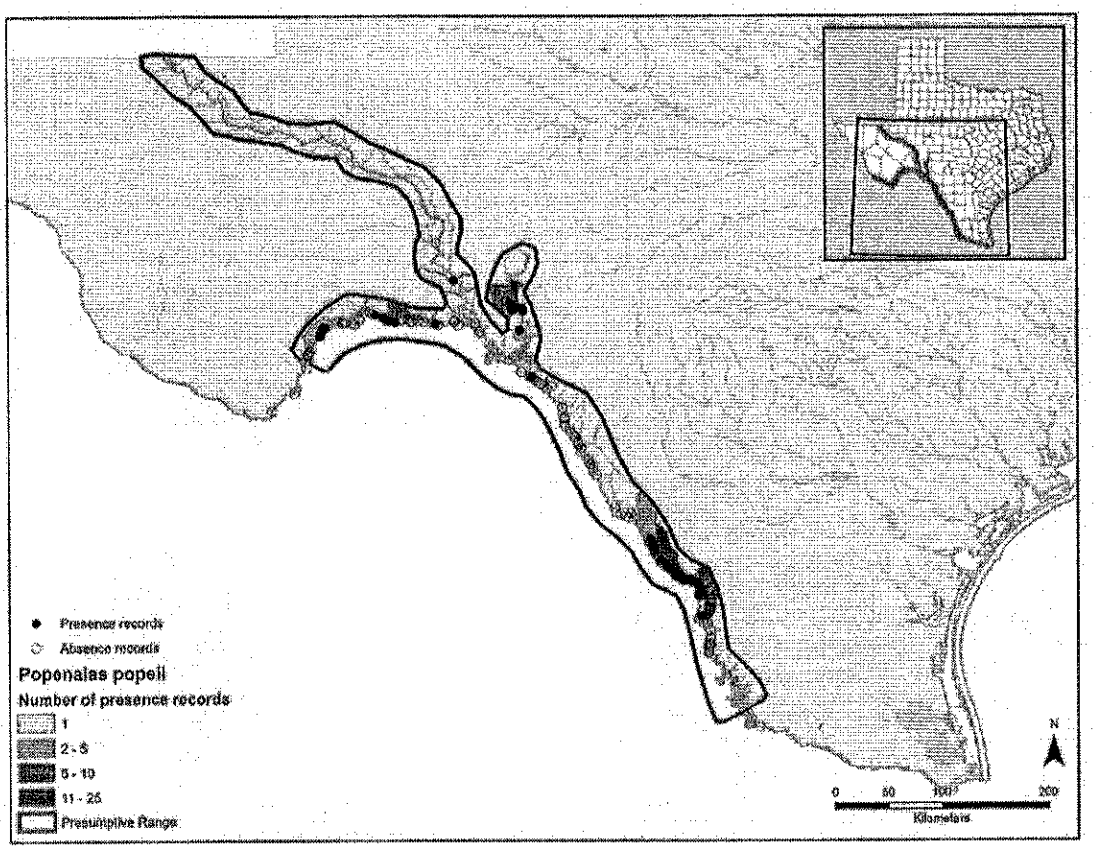

Figure 9. Map of prevalence for *Popenaias popeii* (Texas hornshell) in the Rio Grande. Shaded circles denote presence and unshaded circles indicate absence for *P. popeii*. Survey sites shown are from 2000 to present and are taken from the present study plus those obtained from academic, state, and federal agencies. HUCs are colored based on the number of times *P. popeii* was detected in a given HUC.