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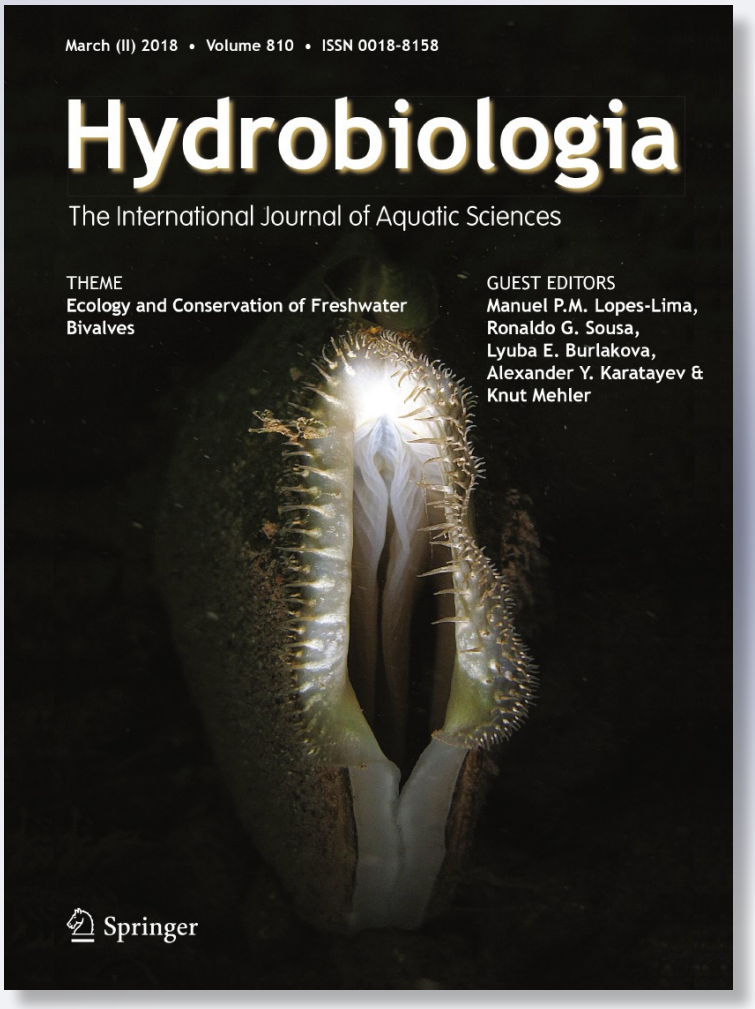

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FRESHWATER BIVALVES

Reconstructing historical range and population size of an endangered mollusc: long-term decline of *Popenaias popeii* in the Rio Grande, Texas

Alexander Y. Karatayev · Lyubov E. Burlakova · Thomas D. Miller · Mary F. Perrelli

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Abstract Although freshwater molluscs in the order Unionoida are considered one of the most endangered groups of animals in the world, sufficient data on their status are lacking for most species. As a result, a species may become rare, endangered, and even extinct before the first population assessment is conducted. This is especially true for endemic species, particularly those limited to remote regions with difficult access. We studied the current distribution and population densities of *Popenaias popeii* endemic to the Rio Grande drainage in Texas, and developed a method to evaluate changes in the population's size and distributional range over the last 100 years. Sampling over 250 sites in four rivers that constitute the entire historical range of *P. popeii* in Texas, we found that this species has likely been extirpated from two rivers. The total length of the rivers populated by this mussel has declined by 75%, and the total *P. popeii* population size has declined by 72%. The remaining population of this species in the Rio Grande is fragmented, with only one 190-km stretch still supporting high densities. The developed approach could be used for other rare freshwater molluscs to reconstruct their historical range and population size.

Keywords Unionidae · Distribution · Rare species · Conservation · Impoundment · Pollution

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Introduction

Globally, molluscs (both freshwater and marine Bivalvia and Gastropoda) represent 42% of all extinct

animals and 25% of those critically endangered (IUCN, 2015). In North America, three quarters of all freshwater mollusc species are considered imperiled or extinct, exceeding the imperilment levels of fish (39%) and crayfish (48%) (Williams et al., 1993; Johnson et al., 2013). Nevertheless, at a global scale, only 8% of all molluscs have been evaluated for extinction risks, compared to 100% of mammals and birds, 87% of amphibians, and 39% of fish (IUCN, 2015). This lack of attention is striking because the vanishing mollusc species not only constitute an integral part of the biological diversity in threatened freshwater ecosystems, but also provide important ecological functions and services (Aldridge et al., 2007; Vaughn, 2010).

Significant declines in population size or geographical range are the major criteria used to categorize a species as endangered (Endangered Species Act, 1973; IUCN, 2014), and all recovery plans therefore advocate the use of quantitative metrics (reviewed in Ahrens & Pine, 2014). To assess the degree of endangerment, decline, or recovery of a species, reliable measures of their populations are needed. However, the status and trends of unionid mussel populations are often described qualitatively, e.g., "poor," "declining," "stable," etc., and quantitative assessments are rare (Strayer et al., 1996). Indeed, among all Bivalvia species, the most threatened and data deficient are in the order Unionoida (IUCN, 2015). Lack of information on essential parameters for these species, such as distribution range and population size, greatly hampers the assessment of their conservation status. As a result, mussel species may become rare, endangered, and even extinct before the first population assessment is conducted (Strayer et al., 1996; Burlakova et al., 2011a). This is especially true for endemic species which have a limited range restricted to remote regions with difficult access. In contrast to most other invertebrates, however, dead molluscs (particularly unionid bivalves) leave large calcareous shells that may remain in sediments for decades, providing evidence of former populations and helping to reconstruct historical ranges.

In Texas, 40% of all freshwater mussel species are of conservation concern—much higher than for all other animal groups—and over 90% of these species are endemic to Texas, or to even smaller areas within the state (TPWD, 2005). The Rio Grande endemic *Popenaias popeii* (Texas hornshell) was first described by Lea (1857) as *Unio popeii* from the Devils River in Texas and the Río Salado in Mexico. *P. popeii* is known exclusively from lotic waters and disappears from river stretches after construction of impoundments (Metcalf & Stern, 1976; Neck & Metcalf, 1988; Karatayev et al., 2012). In the Black River (a shallow, narrow stream that runs over travertine bedrock) in New Mexico, adult *P. popeii* are found in small-grained sediments accumulated in undercut riverbanks, crevices, shelves, and at the bases of large boulders (USFWS, 2013). In the Rio Grande, adult *P. popeii* are usually found in low-flow refuges under large boulders, where sand and clay seams provide substrates for mussels (Karatayev et al., 2012), while habitat preferences of juvenile *P. popeii* have not been described (Carman, 2007). *P. popeii* longevity in the Black River exceeds 20 years and maximum recorded mussel length was >123 mm (Carman, 2007; Inoue et al., 2015). Although laboratory studies indicate that *P. popeii* is a host generalist, only three species of fish (*Carpiodes carpio*, *Moxostoma congestum*, and *Cyprinella lutrensis*) have been identified in the field as the primary hosts, carrying over 99 percent of all glochidia (Levine et al., 2012; USFWS, 2013).

The distribution range of *P. popeii* in Texas historically (in nineteenth century) was restricted to the Rio Grande drainage, including the Pecos and Devils rivers and Las Moras Creek (Singley, 1893; Taylor, 1967; Burlakova et al., 2011a, b; Karatayev et al., 2012). Although two dead *P. popeii* shells were reported from the South Concho and Llano rivers in Texas outside the Rio Grande drainage (Strenth et al., 2004), there is no evidence that these records represent extant populations. Outside Texas *P. popeii* was reported from New Mexico, where its population declined by 88% (Lang, 2001; Carman, 2007; Inoue et al., 2014), and in several Mexican tributaries (Simpson, 1914; Johnson, 1999; Strenth et al., 2004). Singley (1893) described *P. popeii* as a "rare shell", Strecker (1931) reported that the species "seems to be rather scarce", Stansbery (1971) defined it as "rare and endangered", and Neck (1984) included *P. popeii* in his list of restricted and declining species of Texas. According to Howells (2001), no live *P. popeii* have been found in the Rio Grande drainage in Texas from the mid-1970s. Because of this dramatic decline, *P. popeii* has been added to the state's list of threatened species (Texas Register, 35, 2010), is considered as critically

endangered by IUCN (www.iucnredlist.org/details/17992/0), and is a candidate for listing under the federal Endangered Species Act since 2004 (Federal Register, 79, 2014; USFWS, 2015).

Nevertheless, live *P. popeii* were found in 2002–2008 in the Rio Grande River (45 mussels), and in the Devils River in 2008–2011 (7 individuals), confirming that the species is still present in Texas (Karatayev et al., 2012). In 2011, 604 live *P. popeii* were found at La Bota near Laredo (where the local population was estimated at about 8700 mussels), suggesting that the Rio Grande still supports a viable population of *P. popeii*. Inoue et al. (2015) showed that *P. popeii* in the Rio Grande drainage are genetically disconnected from the Black River population and likely comprises a separate evolutionarily significant unit, elevating the importance of its protection. Unfortunately, our ability to monitor changes in its historical distribution and protect this species is restricted because a quantitative assessment of the *P. popeii* population in Texas has never been conducted due to the rarity of this species. The goals of this paper are to reconstruct the historical range and population size of the Rio Grande endangered endemic unionid *P. popeii* to assess its long-term decline and current level of imperilment.

Methods

Study area

We studied the Rio Grande and all three of its tributaries in Texas where *P. popeii* historically occurred, including the Pecos and Devils rivers and Las Moras Creek (Fig. 1). The Rio Grande (total length: 2,830 km, including 1,470 km in Texas) is one of the longest rivers in North America, which flows across seven physiographic provinces, from mountain forests and high mountain deserts to desert shrub and grassland (Dahm et al., 2005). In Texas, the Rio Grande forms the border between the United States and Mexico and has been intensively used by both countries during the last century for irrigation, industrial, and domestic water consumption (Dahm et al., 2005; Wong et al., 2007). Due to water over-extraction, less than a fifth of the Rio Grande's historical flow now reaches the Gulf of Mexico; the riverbed between El Paso and Presidio, Texas, frequently is dry, and in 2001 and 2003 the river failed to reach the Gulf of Mexico (Edwards & Contreras-Balderas, 1991; Contreras-Balderas et al., 2002; Dahm et al., 2005; Wong et al., 2007; Douglas, 2009). In addition, the river suffers from persistent droughts, an increase in border populations, and subsequent increases in the water pollution and wastewater discharge (Dahm et al., 2005; Wong et al., 2007; Douglas, 2009). The river flow is regulated by the Amistad and Falcon dams (completed in 1969 and 1953) that impound the Rio Grande for irrigation and flood control along with several additional low-head dams or weirs.

The Pecos River (total length 1,490 km, including 679 km in Texas) is the largest Rio Grande tributary in the United States. It flows from Mora County, New Mexico, southeast through Texas where it joins the Rio Grande. The river runs through flat, semi-arid lands along the upper section, and through canyons and desert terrain in the lower reaches. Red Bluff Reservoir, a small lake established for hydroelectric power, is located near the Texas–New Mexico border. Below the Red Bluff Reservoir, the Pecos contains only a very limited flow of water, and often lies dry while passing through an arid region of West Texas where rainfall is sporadic and minimal (annual precipitation of 28 cm, Dahm et al., 2005). In the nineteenth century, the river was fast moving and deep (20–30 m wide and 2–3 m deep), with slightly saline taste (Pope, 1854 cited in Hoagstrom, 2003; Hayter, 2015). Several hydrological changes initiated in the 1880s, including diminished streamflow due to aquifer depletion, reduced floods, groundwater overdraft, and increased prevalence of natural, high-salinity groundwater, contributed to the increase in streamflow salinization of up to 20,000 μmhos cm^{-1} (Hoagstrom, 2003, 2009). Since most of the industrial and agricultural activities in this area depend solely upon the Pecos River, many factors such as water overdraft and increasing salinity (Campbell, 1959; Davis, 1987; Gregory & Hatler, 2008), contaminated runoff, oil field pollutants, and blooms of toxic algae caused a deterioration in water quality (TPWD, 1974).

In contrast, the Devils River is considered one of the cleanest, naturally flowing streams remaining in Texas due to its remote location, canyons and rugged desert terrain, low population, and lack of development (TPWD, 1974). It begins in Sutton County, and flows southwest for 151 km into the Amistad Reservoir. Due to the arid nature of the region, the Devils

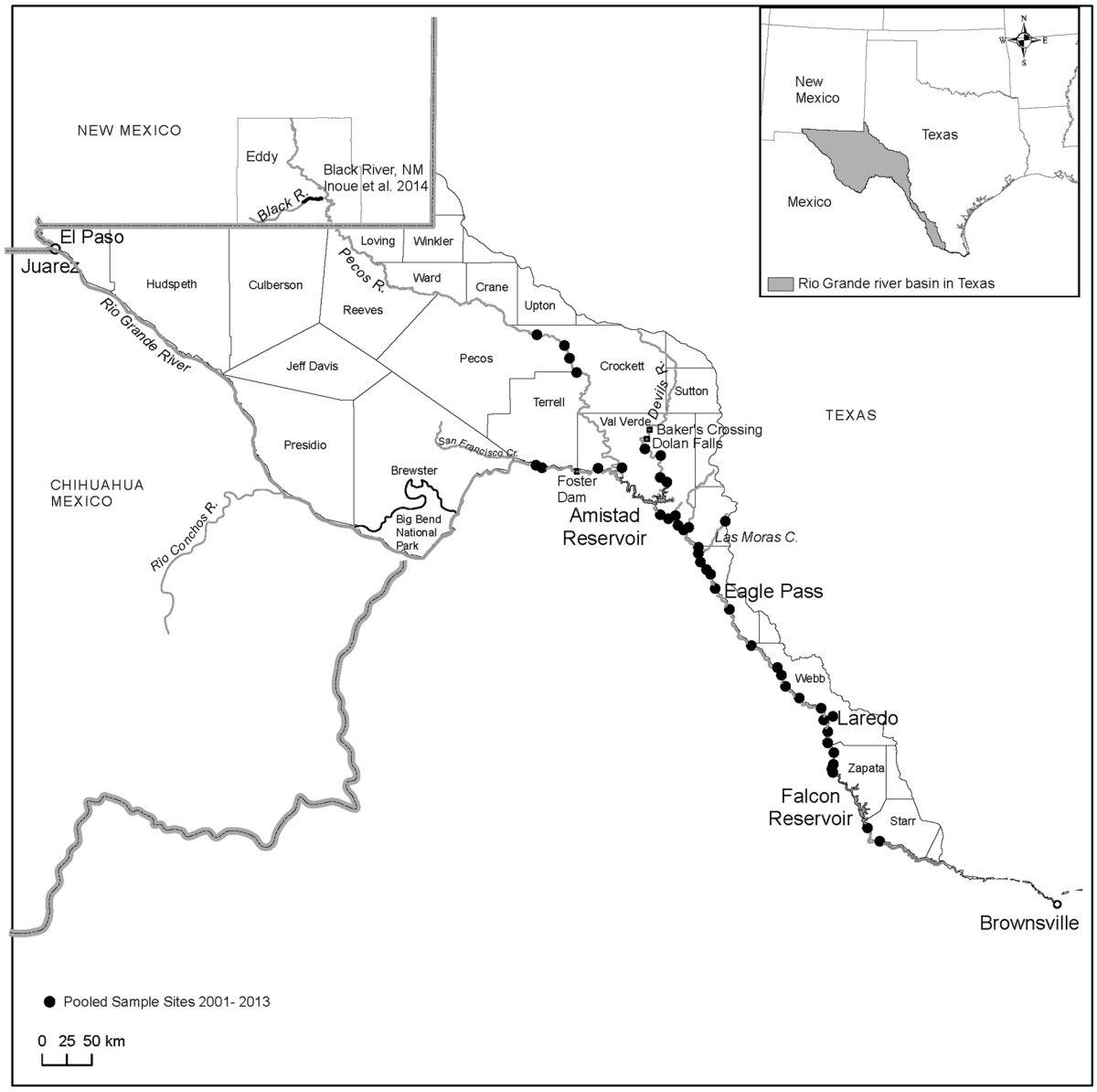

Fig. 1 Map of the Rio Grande basin in Texas with 42 pooled sampling sites surveyed during 2001–2013. Texas counties, major cities, reservoirs, and rivers are indicated

River is intermittent in its upper reaches, and in some stretches flows completely underground. Downriver of Dolan Falls, a 4.6-m-tall natural waterfall located app. 80 km from the river mouth, the river begins to widen and deepen gradually, with an abundance of long, deep pools alternated with rapids. The terminal 30-km stretch of the Devils River is regularly flooded by the Amistad Reservoir. In addition, several low-head dams restrict water flow in the river.

The headwaters of Las Moras Creek are formed by artesian Las Moras Springs located in Fort Clark, Kinney County, Texas. The springs filled a swimming pool built in the beginning of the twentieth century (Haenn, 2002). Las Moras Creek runs 60 km downstream to the confluence with the Rio Grande in Maverick County. The flow rates between 1896 and 1978 ranged from a high of 1.7 m^3 per second (m^3 s^{-1}) in 1899 to lows of 0.16 and 0.10 m^3 s^{-1} in

1964 and 1971, respectively. In these 2 years, the springs dried up completely for a time (Brune, 1975).

Data collection

To assess the distribution, density, and long-term population dynamics of *P. popeii* in the Rio Grande drainage within Texas, we used both field studies and historical data analysis. From 2001 to 2013, we surveyed 250 sample locations ("sites") within the Rio Grande system, including 162 sites studied in 2001–2011 (preliminary analysis of these data published in Karatayev et al., 2012) and 92 sites sampled in 2011–2013. Our recent study, however, was much more focused on the quantitative population assessment than Karatayev et al.'s (2012) study, which was mostly presence/absence survey. Since many of the sites were located close to each other, for calculation of mussels' occurrence (Figs. 1, 2) we pooled all 250 sites into 42 larger sites ("pooled sites") by rounding their latitude and longitude coordinates to the first decimal degree (e.g., 30.0 and 101.1). The majority (over 580 km) of sites in remote areas of the Rio Grande, the Devils, and lower Pecos rivers were surveyed using an airboat and/or canoes. In the Rio Grande where *P. popeii* was clearly associated with certain habitat types (see below), we used stratified sampling design primarily surveying these habitats. In the Devils River and the lower Pecos River, we used systematic sampling (app. at each 0.5 and 2.5 km, respectively). In other areas, due to the limited accessibility (only 2% of the lands remain in public ownership, TPWD, 1974), we used opportunistic sampling, locating survey sites within state parks, near public boat ramps, or based on accessibility from roads. Landowner permission was acquired from each property owner, when surveys were conducted from private land, before entering the property. The work was carried out with an appropriate Scientific Research Permit issued by the Texas Parks and

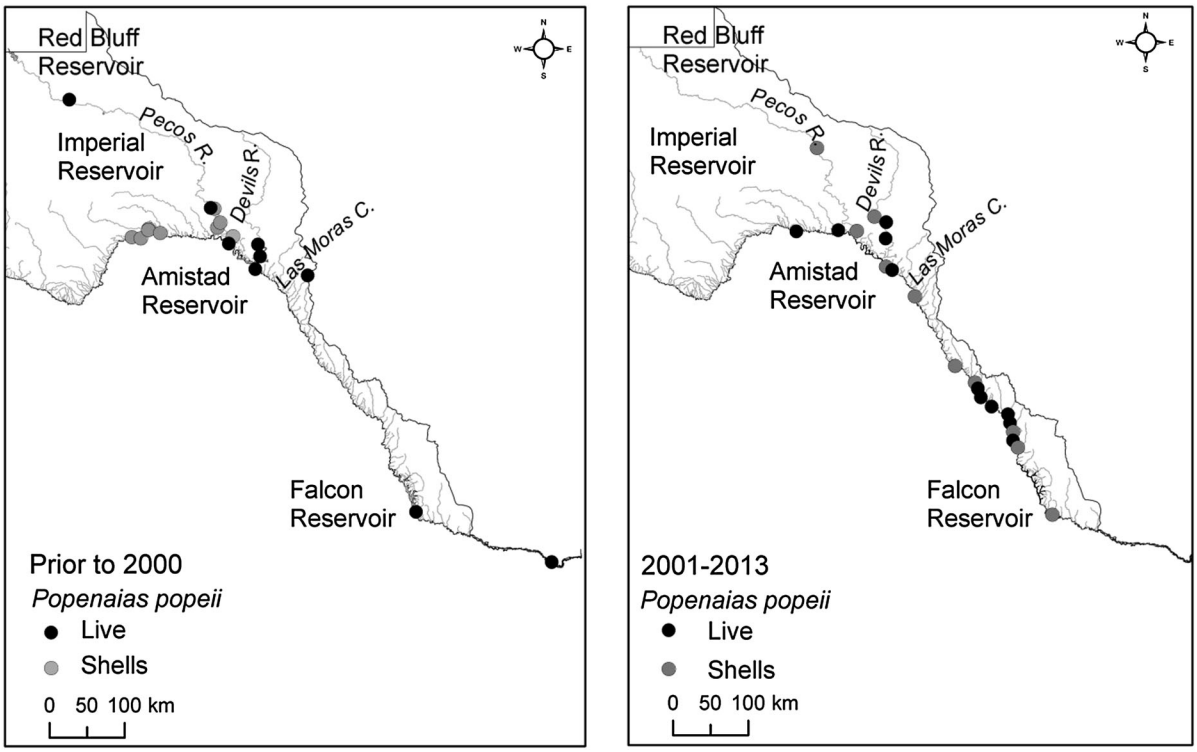

Fig. 2 Map of the Rio Grande basin in Texas with sites where live and/or dead shells of *Popenaias popeii* were found prior to 2000 (based on data from: Singley, 1893; Cockerell, 1902; Strecker, 1931; Taylor, 1967; Metcalf, 1974, 1982; Murray, 1975; Metcalf & Stern, 1976; Neck, 1984; Neck & Metcalf, 1988; Howells, 1994, 2001; Howells et al., 1996, 1997; Johnson, 1999; Karatayev et al., 2012, and museum collections) and from 2001 to 2013 (pooled sites, authors' data)

Wildlife Department, National Park Service Scientific Permit for Big Bend National Park, and Amistad National Recreational Area Research Permit.

We collected both live and dead mussels at each sampling location by hand (tactile searches), by snorkeling (at most of the sites), wading in low water, or SCUBA diving. We used reconnaissance sampling (timed search) at all sites (Strayer et al., 1997; Vaughn et al., 1997). If live *P. popeii* were present in numbers allowing for density estimates (>0.1 m^{-2}), quantitative methods were used for assessments of density (Miller & Payne, 1988; Vaughn et al., 1997). Collected live mussels and shells were counted and measured with calipers to the nearest mm, and then live mussels were carefully bedded back into the sediment from which they were taken. Shell condition of dead mussels was recorded for each shell. Shells were considered very recently dead if soft tissue remains attached to the shell and recently dead if internal and external colors were not faded (nacre still lustrous), or somewhat faded. Shells with most or all of the internal coloration and gloss faded, shell periostracum absent, or aged and flaking, were considered long dead. Shells with little or no epidermis, with nacre and entire shell faded white, often with extensive signs of erosion, staining, and calcium deposition were considered subfossil.

Data analysis

Geographic coordinates for sampled locations were mapped in ESRI ArcGIS 10.1. The 2010 stream data published by the Texas Commission on Environmental Quality was used as the base layer for the analysis. This is a general purpose data layer at a scale of 1:250,000. The approximate length (km) of the current ranges for the sampled areas was calculated using ArcGIS.

Devils River

We sampled the Devils River in 2011–2013 from Baker's crossing to the Amistad Reservoir in 2,223 man hours of search effort. Due to low density of mussels (Table 1), quantitative methods were not applied, and reconnaissance sampling (timed search) was used to reveal the presence of mussels. In 2011–2013, we searched 34 sites totaling 7.15 km along the river and found five live *P. popeii.* Then we

Table 1 Current and historical ranges, density, and population size (mean ± SE) of *Popenaias popeii* in the Rio Grande drainage of Texas

Waterbody	Current range (km) (% from historical)	Historic range (km)	River width (m)	Current density (m^{-2})	Historic density (m^{-2})	Current population, mussels (% from historical)	Historic population, number of mussels
Rio Grande between the Big Bend and Eagle Pass (excluding Amistad Reservoir)	200	n. c.	56.0 ± 3.3	0.00081 ± 0.00041	n. c.	9,029 ± 4,594	n. c.
Rio Grande between Eagle Pass and Laredo	190	190	94.9 ± 4.0	0.0186 ± 0.0040	0.0186 ± 0.0040	335,050 ± 72,709	335,050
Rio Grande excluding the area between Eagle Pass and Laredo	n. c.	810	72.7 ± 2.7	n. c.	0.0118 ± 0.0010	n. c.	693,160
The whole Rio Grande from the San Francisco Creek to Brownsville	390 (39%)	1000	n. c.	n. c.	n. c.	344,078 ± 29,709 (33%)	1,028,209
Devils River	66 (69%)	96	42.5 ± 3.7	0.00081 ± 0.00041	0.00081 ± 0.00041	2,261 ± 1,150 (69%)	3,289
Pecos River	0 (0%)	679	25.5 ± 3.6	0	0.0118 ± 0.0010	0 (0%)	203,809
Las Moras Creek	0 (0%)	60	7.6 ± 1.1	0	0.0118 ± 0.0010	0 (0%)	5,368
Total	456 (25%)	1,835	n. c.	n. c.	n. c.	346,340 ± 29,731 (28%)	1,240,675

n. c. not calculated

calculated the ratio of time search effort (in man hours) spent at each site to the average time effort across all sites. The average ratio on the sites where we found *P. popeii* (0.51 ± 0.11, mean ± standard error here and elsewhere unless noted) indicated that extra effort was not applied to these sites. We then weighed the density by dividing the number of *P. popeii* per area (m^{-2}) at each site per effort ratio at the site. To compensate for potential error associated with difficulty in finding mussels, we adjusted the density by the probability of detection (or correction factor) calculated for this species using an estimate of encounter probability from 3 years of mark-recapture *P. popeii* study in La Bota (0.072 ± 0.009, $n = 9$). Using these data, we estimated the current total population of *P. popeii* in the Devils River considering that the sampled habitat covers 66 km of the upper part of the river not flooded by the Amistad Reservoir. The historical population range and size of *P. popeii* in the Devils River were estimated for a distance of 96 km from the Baker's crossing and the confluence with the Rio Grande.

Rio Grande

The highest population density of *P. popeii* was recorded on the stretch of the Rio Grande from El Indio Dam below Eagle Pass to Laredo, totaling 190 river km, 100 km of which were searched. In the Rio Grande, high concentrations of *P. popeii* (mussels beds) were found at all 15 appropriate habitats (areas with large rocks on top of bedrock) located in this 100-km stretch, with virtually no mussels found between the beds. At six randomly selected *P. popeii* mussel beds, we recorded the total area of the bed and conducted quadrat (from 3 to 15 0.25 m^2 quadrats, depending on the bed area) or area searches (3–4 area searches per mussel bed, areas from 1 to 12 m^2). The average *P. popeii* density at these six mussel beds was 2.04 ± 0.43 m^{-2}. In the other nine mussel beds, we used time searches to confirm mussel presence without quantitative assessment of mussel density. For population estimations, we treated this part of the Rio Grande as two strata: one with mussels (the 15 mussel beds) that occupied about 82,842 m^2 of the river, and the remaining stratum (9,407,158 m^2) between beds where we usually did not detect mussels (only two *P. popeii* were found in such habitats throughout the study). However, as the effort at this mussel-poor strata (quadrat- and time searches at 10 sites) was lower than in the Devils River (34 sites), to correct for potential mussel detection failures, we assumed that their density in the strata was likely similar to the Devils River density (0.0008 ± 0.0004 mussels m^{-2}) (Table 1). The mean overall mussel density at this stretch and its standard error were calculated using mean densities and areas of the strata following formulae for stratified random design (Manly, 2009). To estimate the total population size of mussels between Laredo and Eagle Pass, we multiplied this density by river average width and length (94.9 m, 190 km).

In other parts of the Rio Grande, density of *P. popeii* was very low. In 2008 and 2011, two individual *P. popeii* were found in the river below the Big Bend National Park at John's Marina (south of Dryden, Terrell County). Another single *P. popeii* was found in our survey of 200 km of the river downstream from the Foster Dam (near Langtry, Val Verde County) to the upper reaches of the Amistad National Recreation Area. Two more *P. popeii* were found near Del Rio (Val Verde County). Bottom substrates in this stretch of the Rio Grande were similar to those in the Devils River (mainly bedrock with gravel riffles), and both rivers at these locations have comparable median water flows (International Boundary Water Commission Stream Gauge Data, 2014). Therefore, to calculate the current *P. popeii* density in the stretch of the Rio Grande from the Big Bend National Park (San Francisco Creek mouth) to the upper part of the Amistad Reservoir and near Del Rio (total 200 km), we used the densities estimated for the Devils River (0.00081 ± 0.00041 mussels m^{-2}). The mean overall density (±SE) of *P. popeii* in these two populated stretches of the Rio Grande (0.0118 ± 0.0010 m^{-2}) was calculated following formulae for stratified random design using mean densities and areas of these stretches (Manly, 2009). No live mussels were found between Del Rio and Eagle Pass.

Downstream of El Paso/Juarez area, flow in the Rio Grande is extremely limited (Dahm et al., 2005), and the river may stay dry for several months of the year before it reaches the confluence with Rio Concho. Considering this, as well as the lack of historical records from this area, we excluded the river stretch from El Paso to Big Bend National Park from the currently occupied habitat. Similarly, we excluded from the current range all areas below Laredo as no live *P. popeii* were found in our surveys

downstream from the Laredo Sewage Plant to the Falcon Reservoir.

Historical distribution

To reconstruct the historical range of *P. popeii* in Texas, we used a total of 327 records of live mussels and dead shells from published accounts (Singley, 1893; Cockerell, 1902; Strecker, 1931; Taylor, 1967; Metcalf, 1974, 1982; Murray, 1975; Metcalf & Stern, 1976; Neck, 1984; Neck & Metcalf, 1988; Howells, 1994, 1999, 2000, 2001; Howells et al., 1996; Johnson, 1999; Strenth et al., 2004; Karatayev et al., 2012, and museum collections), and the current study in the Rio Grande and its tributaries. The Rio Grande River water is hard with alkaline pH (Ryu et al., 2005) and thus favors long persistence of spent fairly thick shells of *P. popeii* (Strayer & Malcom, 2007). We made the following assumptions: (1) the historical range of *P. popeii* in Texas corresponds with waterbodies where live or dead shells have been recorded; (2) historically, *P. popeii* were present in the whole river stretch between the two most distant points where live or dead shells have been recorded; (3) *P. popeii* records were considered living unless otherwise stated; (4) year of record was one year prior to publication, unless otherwise stated (excluding papers where museum collections were analyzed and mussels had collection dates on their labels); (5) in the almost pristine Devils River, the historic *P. popeii* population densities were similar to current densities; (6) in the Rio Grande, the historic *P. popeii* population density between Laredo and Eagle Pass (where *P. popeii* are still present in high density in suitable habitat) was similar to the current; (7) in the rest of the Rio Grande, the historic *P. popeii* population densities were similar to the current mean overall density of *P. popeii* in all populated stretches of the river; and (8) similarly, in rivers with extirpated *P. popeii* populations (the Pecos River and Las Mores Creek) the historic population densities were estimated as the current mean overall density of *P. popeii* in the Rio Grande.

Results

Current distribution

A total of 1,801 live *P. popeii* were recorded in our surveys. Live specimens and shells of this species were found at 26 and 43% of the 42 pooled sites sampled, respectively (Fig. 2). The species was most commonly found in crevices under large flat boulders of limestone conglomerates resting on bedrock, where small sediment deposits provide stable substrates for mussels in these flow refuges, with over 10 (and up to 40) individuals found under one rock.

In the Devils River, we found only five *P. popeii* during three intensive surveys in 2011–2013. We estimated the current density of *P. popeii* in this waterbody to be 0.00081 ± 0.00041 m^{-2}, for a total population size of 2,261 ± 1,150 mussels (Table 1).

The density of *P. popeii* in the 190-km stretch of the Rio Grande between Eagle Pass and Laredo was the highest among its entire range (0.0186 ± 0.0040 m^{-2}, Table 1), and the estimated population size on this section of the river was 335,050 ± 72,709 mussels. Between the Big Bend National Park and Del Rio (200 km, excluding the Amistad Reservoir, in which this species has not been found), we estimated a density of 0.00081 ± 0.00041 mussels m^{-2} (the same as that observed in the Devils River), for a total of 9,029 ± 4,594 *P. popeii* in this river stretch. Only long dead and subfossil shells were found at seven sites below the Laredo Sewage Plant waste water discharge (this study; Karatayev et al., 2012), despite the presence of numerous *P. popeii* just 10 m upstream of the discharge site (at the mouth of Zapata Creek, Las Palmas Park) and an abundance of suitable habitat below the plant. Thus, the current estimated population size of *P. popeii* in the Rio Grande was 344,078 ± 29,709 mussels (Table 1).

No live *P. popeii* were found in the Pecos River during our study. Long dead and subfossil shells were extremely abundant in the lower reaches of the river, where live mussels were reported by Metcalf (1982) prior to the area being flooded by the Amistad Reservoir. In addition, one fragment of a *P. popeii* valve (evaluated as recently dead) was found in 2011 at one of the four surveyed sites on the Pecos River in Pecos County (near Iraan). Our study also did not reveal any live mussels or even dead shells of *P. popeii* in the Las Moras Creek.

Historical range and population size

Based on historical records (Singley, 1893; Cockerell, 1902; Strecker, 1931; Taylor, 1967; Metcalf, 1974, 1982; Murray, 1975; Metcalf & Stern, 1976; Neck,

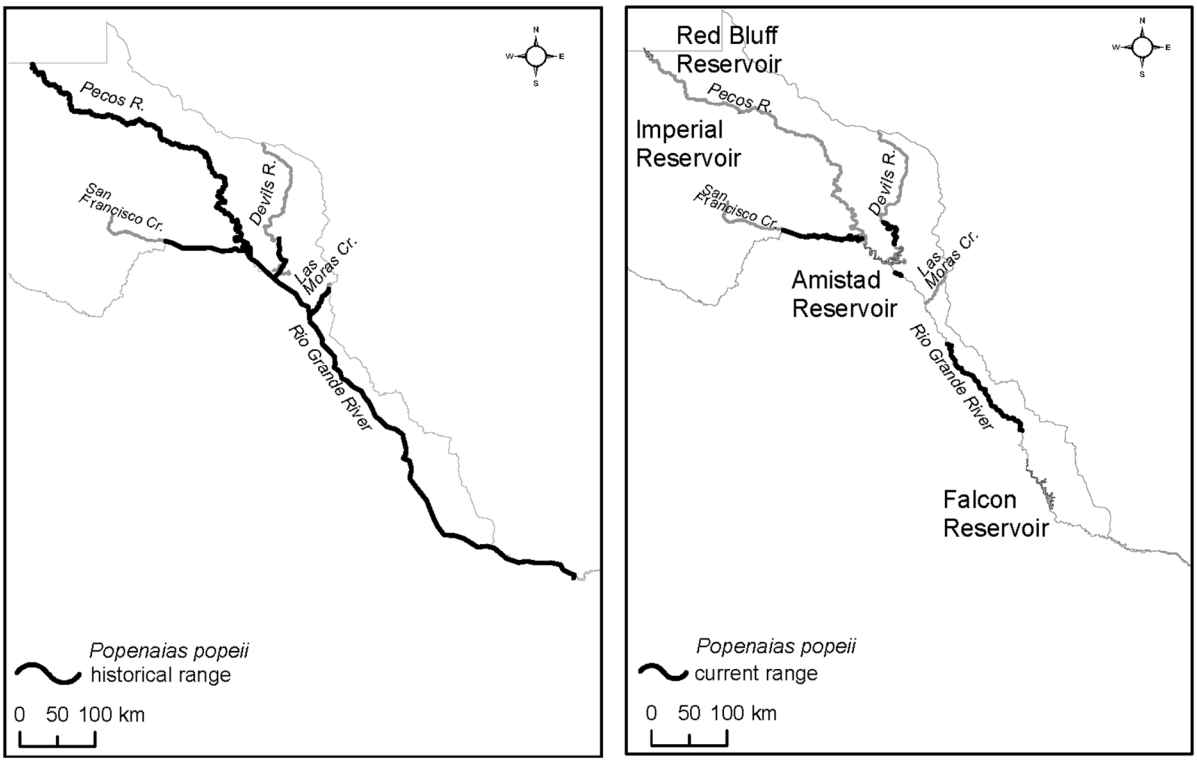

Fig. 3 Map of the Rio Grande basin in Texas with historical and current range of *Popenaias popeii* in Texas

1984; Neck & Metcalf, 1988; Howells, 1994, 2001; Howells et al., 1996, 1997; Johnson, 1999, and museum collections) and our shell findings, *P. popeii* in the past likely occurred throughout the 1,000-km stretch of the Rio Grande from the mouth of San Francisco Creek in the Big Bend reach (Brewster County) to Brownsville, near the Gulf of Mexico (Figs. 1, 3). According to Metcalf & Stern (1976), no living or fossilized unionids were ever reported in the Rio Grande above the mouth of the Rio Conchos. Currently, *P. popeii* persists in only two fragments of the Rio Grande: between Big Bend National Park and Del Rio (excluding the Amistad Reservoir), and between Eagle Pass and Laredo—which constitutes only 39% of the species' historical range in the river (Fig. 3). We estimated the historical population size of *P. popeii* in the Rio Grande at about 1,028,200 mussels, which indicates that the current abundance of this species in the river is at only 33% of its historical levels (Table 1).

In the Devils River, *P. popeii* historically were found only in the lower reaches (in Val Verde County, Singley, 1893; Neck, 1984), which are currently flooded by the Amistad Reservoir and are no longer suitable for *P. popeii* (Figs. 1, 3). As the remaining length of the river is almost in pristine conditions, being one of the cleanest, naturally flowing streams remaining in Texas (TPWD, 1974), we assumed that the historical *P. popeii* density throughout the river was similar to that observed in the present study (0.00081 ± 0.00041 mussels m^{-2}). This is likely an underestimation as in the past mussels were more abundant near the river's confluence with the Rio Grande. Although the lower reaches of the river are now flooded by the reservoir, we estimated the historical range of *P. popeii* as the distance between our most upstream record of the species and the mouth of the river (Figs. 2, 3; Table 1). According to these assumptions, the Devils River historically supported a total of 3,289 *P. popeii* (Table 1).

In the Pecos River, *P. popeii* was reported by Metcalf (1982) from the lower reaches which were later flooded by the Amistad Reservoir. In addition, in the past mussels were recorded in this river in New Mexico (Cockerell, 1902; Metcalf, 1982; Lang, 2001), and are still abundant in one of its tributaries (the Black River, Lang, 2001, 2010; Inoue et al., 2014).

Therefore, we suggest that the entire span of the Pecos River in Texas was previously populated by *P. popeii*. We estimated its historical density as the species' current mean density across all populated stretches of the Rio Grande (0.0118 ± 0.0010 m^{-2}). According to this assumption, the total number of *P. popeii* that the Pecos River in Texas supported historically was 203,809 (Table 1); this is likely an underestimate of the species' historical abundance since the current total population of *P. popeii* in a much shorter stretch of the Black River (14 vs. 679 km) is 48,006 mussels (Inoue et al., 2014).

In the Las Moras Creek, *P. popeii* were first recorded in 1892 (Taylor, 1967), and according to Cockerell (1902) they were abundant in this creek near Fort Clark at the end of nineteenth century. However, extensive, repeated surveys of the Las Moras Creek in 1971, 1973, and 1975 found no living *P. popeii* (Murray, 1975). Our study also did not reveal any live mussels or even dead shells. To reconstruct the former density of *P. popeii* in the Las Moras Creek, we used the mean (overall) density in the currently populated stretches of the Rio Grande (0.0118 ± 0.0010 m^{-2}). Based on this assumption, we estimated the historical abundance of *P. popeii* in the Las Moras Creek at approximately 5,368 mussels (Table 1). Again, this estimate of the historical population size is likely very conservative since a 4× shorter stretch of the environmentally similar Black River is estimated to contain 48,006 molluscs (Inoue et al., 2014).

Discussion

Since the first description of *P. popeii* by Lea (1857), the species was always considered rare, declining, or even endangered (Singley, 1893; Strecker, 1931; Stansbery, 1971; Neck, 1984). Before the beginning of our study, less than 200 individuals have been recorded across all previously published studies of this species in Texas, and a quantitative assessment of the species has never been conducted. The recent discovery of a relatively large population of *P. popeii* in the Rio Grande above Laredo and a small population in the Devils River proved that the species still exists in Texas (Karatayev et al., 2012). Being endemic to the Rio Grande drainage, *P. popeii* has been restricted to only a few rivers over the last century, and its formerly continuous distribution across this range in Texas has been fragmented and reduced to few isolated populations. Current population densities of *P. popeii* in Texas ranged from 0.0008 m^{-2} in the Devils River to 0.019 m^{-2} in the Rio Grande (with a maximum of 6.5 m^{-2} in mussel beds). These densities are similar to those of other rare unionid species like *Alasmidonta heterodon* ranging from 0.001 to 0.0001 m^{-2} (a nearly undetectable level) to 0.04 m^{-2} (Strayer et al., 1996). As suggested by Strayer et al. (1996), such low population densities may be either a natural feature of *A. heterodon* populations, or may have resulted from pervasive human influences which started before first systematic mussel observations began (Strayer et al., 1996). Either explanation could account for the *P. popeii* distribution in the Devils River.

Using historical data on the distribution of *P. popeii*, indications of past presence from shells collected during our study, and density estimates in recently discovered populations, we were able to reconstruct the historical distribution range and population size of this species in Texas (Fig. 3). We found that *P. popeii* has been extirpated from two of four rivers, the total length of the river stretches populated by the mussel has declined by 75%, and we estimate that the total *P. popeii* population size has reduced to 28% of its historical level. During our study, we never found live *P. popeii* outside its historical range.

Potential uncertainty

We recognize the limitations among some of our current and historical population size estimates. Currently, the very low densities of *P. popeii* in the Devils River preclude an accurate assessment of the actual population size. For example, despite our extensive surveys, there is a chance that we overlooked small, high-density pockets of *P. popeii* in this river. In addition, the remote stretch of the Rio Grande between the Big Bend National Park and the Foster Dam is understudied (due to very limited access) and may still support areas with high *P. popeii* densities. At the same time, however, Devils River accounts for only a modest fraction of both the current and historical *P. popeii* population (0.7 and 0.3%, respectively).

We are quite confident in our estimation of the historical distribution range of *P. popeii* in Texas, as it is based on numerous published records, museum collections, and the current presence of dead shells. It is also evident that this species has been extirpated

from Las Moras Creek and the Pecos River, although our discovery of one fragment of a recently dead shell in 2010 suggests that *P. popeii* may still exist in the latter waterbody, particularly in the lower reaches. The estimated decrease of the overall range of this species in Texas (75%) is similar to concurrent declines in New Mexico, where this species currently occupies about 12% of its historic range (Lang, 2001; Carman, 2007).

In contrast to the species distribution range, our estimation of the historic *P. popeii* population size relies more strongly on a suite of assumptions due to the lack of historic quantitative data. However, while the range of *P. popeii* in Texas clearly decreased over the last century (Karatayev et al., 2012), a quantitative assessment of this decline is extremely important for conservation purposes, and a significant decline in population size is among the major US FWS and IUCN criteria in listing endangered species (Endangered Species Act, 1973; IUCN, 2014). Moreover, decline in geographic distribution may be a poor proxy for changes on overall population size if a species presence (e.g., density) varies widely across habitats or different systems, as in the case of *P. popeii*. Therefore, in this study we have made an attempt to go beyond qualitative descriptions of population decline by developing an approach to approximate the historic *P. popeii* population size. Given the high uncertainty of this estimate, we additionally calculated the lowest and the highest reasonable assessments of *P. popeii* historic abundance. To estimate the lowest abundance, we assumed that mussel density at the 190-km stretch of the Rio Grande between Eagle Pass and Laredo was similar to its current level (0.0186 m^{-2}), while in the Pecos River, the Las Moras Creek, and in the rest of the Rio Grande (810 km), historic densities were similar to the lowest *P. popeii* densities currently seen (0.0008 m^{-2}). We used the same low-density estimate for the Pecos River and Las Moras Creek. To estimate the highest abundance, we assumed that the historic density in the whole populated stretch of the Rio Grande (1,000 km), the Pecos River, and Las Moras Creek was similar to the current high density in the Rio Grande between Eagle Pass and Laredo (0.0186 m^{-2}). As the Devils River is still in a nearly pristine condition, in both estimates we assumed that the historic *P. popeii* abundance was similar to its current levels. Using these scenarios, the whole historic population of *P. popeii* in Texas might range from 600,655 to 1,884,921 mussels, corresponding to a 43–82% loss of the population.

Conservation and management

The most efficient means to secure the viability of existing unionid populations is by applying the knowledge of their distribution, biology, and ecology toward reducing and preventing threats through regulatory mechanisms and habitat restoration programs (USFWS, 2003).

As a first step, information on distribution and population size is required to define conservation priorities. Our 2001–2013 surveys of *P. popeii* in Texas, in combination with recent surveys of the Black River in New Mexico (Inoue et al., 2014), have provided sufficient information on the current population size and range of this species in the USA and, most importantly, on the historical changes in populations in the last 100 years. Again, the species currently occupies only 12 and 25% of its historic range in New Mexico and in Texas, respectively. In Mexico, *P. popeii* is known from several tributaries of the Rio Grande, the Río Salado, and several distinct drainages, including Ríos Pánuco and Valles (Simpson, 1914; Johnson, 1999; Strenth et al., 2004). Although the current status of the species in its whole range in Mexico is unknown (Smith et al., 2003; USFWS, 2013), surveys conducted in the Rio Sabina and the Rio Salado did not reveal any live *P. popeii* (Strenth et al., 2004), suggesting that the Mexican population experienced similar decline. Therefore, we suggest that over the last century, *P. popeii* has faced population fragmentation, local extirpation, and dramatic overall decline in size across its whole range of distribution. This confirms the evaluation of *P. popeii* by IUCN as critically endangered, as the species is facing a high risk of extinction in the wild.

Decline in population size is the first among five quantitative criteria used to determine whether a taxon is threatened (IUCN, 2014). The measure of species' area of occupancy is important for estimating species' decline and is usually obtained by counting the number of occupied cells in a uniform grid (commonly used grid size is 2 km, a cell area of 4 km^2) which covers the entire range of a taxon, and then tallying the total area of all occupied cells (IUCN, 2014). However, we note that grids do not have much ecological meaning for taxa living in "linear" coastal or riverine

habitats (IUCN, 2014). For example, *P. popeii* (in contrast to, for example, amphibians or insects) does not occupy small tributaries or wetlands. Thus, the area cell approach, although useful while evaluating imperilment levels of different kinds of species, grossly overestimates the area of occupancy for freshwater mussels. The method we used for calculating changes in the historical species range is more appropriate for freshwater molluscs with very restricted "linear" habitat ranges. Such linear populations are especially vulnerable to loss because they have no spatial refuge from threats occurring upstream of the population or in the watershed (Strayer et al., 1996) and are also highly prone to fragmentation (Fagan, 2002).

Population fragmentation is another criterion for determining species conservation status (IUCN, 2014). A taxon is considered to be severely fragmented if most (>50%) of its total area of occupancy is in habitat patches that are separated from other habitat patches by a distance larger than the dispersal distance of the taxon (IUCN, 2013). Although laboratory studies described *P. popeii* as a host generalist (24 physiological fish host species identified; Lang, 2001, 2004), Levine et al. (2012) found that in the wild, *P. popeii* uses only a small subset of all potential hosts which occur in the Black River. In particular, *Carpiodes carpio*, *Moxostoma congestum*, and *Cyprinella lutrensis* represented 80% of all individual fish infected and carried over 99% of glochidia. Of these hosts, the small-bodied *C. lutrensis* was the only species infested consistently and exhibited the highest prevalence (30%) (Levine et al., 2012). Only the crevice spawner *C. lutrensis* was abundant among the 629 fish caught in the Rio Grande near Laredo in the summer of 2012 (authors' unpublished data).

Impoundments can also fragment the habitat of *P. popeii* host fish by limiting their dispersal and recolonization (Matthews & Marsh-Matthews, 2007) as all three common fish hosts species reported from the Black River do not have long-distance dispersal (their separation distance for suitable habitat is <15 km, NatureServe, 2014). Since fish hosts are the main vector for *P. popeii* dispersal, the considerable gaps (>40 km) among the populated segments on the Rio Grande and the Devils River due to the presence of the Amistad Reservoir are much larger than the dispersal distance of the species. Therefore, the *P. popeii* population on the Rio Grande drainage may be severely fragmented.

Identifying direct threats to mussel habitats is the next step that needs to be considered in conservation planning. Globally, major threats to freshwater biodiversity (including bivalves) include fragmentation, degradation, and loss of habitat, overexploitation, pollution, introduction of invasive species, and climate change (Dudgeon, et al. 2006; Geist, 2011). The primary threats to *P. popeii* identified by the U.S. Fish and Wildlife Service are habitat alterations such as streambank channelization, impoundments, and diversions for agriculture and flood control; contamination of water by oil and gas activity; alterations in the natural riverine hydrology; increased sedimentation and flood pulses from prolonged overgrazing; and loss of native vegetation (Federal Register, 78, 2014).

Water over-extraction

Water over-extraction is responsible for the extinction of *P. popeii* both in the upper and lower reaches of the Rio Grande. Water diversion from the Rio Grande is so high that the riverbed between El Paso and Presidio/Ojinaga often lies dry (Dahm et al., 2005; Wong et al., 2007; Douglas, 2009); and in 2 years, the river failed to reach the Gulf of Mexico (Dahm et al., 2005). The flow rate of the Las Moras Springs (headwaters of Las Moras Creek) decreased between 1896 and 1978 by an order of magnitude, and in 1964 and 1971 it dried up completely for a period of time (Brune, 1975). Similarly, the Pecos River, which was once a critical source of water in the Trans-Pecos region in Texas, has dwindled to a trickle and is often dry in some areas due to water over-extraction (Gregory & Hatler, 2008).

Impoundments

P. popeii is a lotic species and is not found in reservoirs (Metcalf, 1982; Neck & Metcalf, 1988; Karatayev et al., 2012). Construction of the Amistad and Falcon reservoirs in the Rio Grande turned large stretches of mussel habitats into unsuitable environments, resulting in severe population fragmentation. Impoundments also caused extirpation of *P. popeii* from the lower reaches of the Pecos and Devils rivers where it was previously reported (Singley, 1893; Metcalf, 1974, 1982; Neck, 1984).

Water pollution and salinization

P. popeii was abundant in the Rio Grande 10 m above wastewater discharges from Laredo and Nuevo Laredo wastewater treatment facilities, but absent across a 40-km stretch of the river below the discharge, despite an abundance of suitable habitats. Several live individuals of common unionid species were found only 40 km below Laredo, perhaps sourced from the inflowing Dolores Creek below the Zapata County line, but no live *P. popeii* was found there. According to Murray (1975), *P. popeii* was extirpated from the Las Moras Creek due to the removal of aquatic vegetation, the paving of a portion of the spring, and the chlorination of the spring headwater, which was converted into a swimming pool. High salinity seems to be the major factor limiting *P. popeii* in the Pecos River along with water over-extraction and impoundments. According to Lang (2001), this species shows behavioral signs of physiological stress followed by death at a salinity of 7.0 ppt, which is similar to salinity in the Pecos River (ranges from 6.0 to 7.0 ppt) downstream of its confluence with the Black River in New Mexico (Lang, 2001). Salinity levels are even higher (up to 12 and 20 ppt) in upstream parts of the Pecos River running through Texas (Hoagstrom, 2009).

The next important step in species protection is to identify the most important drainages and localities having viable populations of the threatened species. Our studies identified that the highly populated habitat left in the Rio Grande is the 190-km river stretch between Eagle Pass and Laredo, which also supports another rare endemic Rio Grande mussel *Truncilla cognata*. This large *P. popeii* population is viable and recruiting (Karatayev et al., 2012) and therefore requires priority protection. Although a section of the Rio Grande in and above Laredo has the status of a mussel sanctuary (where mussel harvesting is prohibited, Texas Register, 31, 2006), additional protection is urgently necessary as any activities altering water flow could negatively impact the remaining habitat of *P. popeii*. The population above Amistad Reservoir is smaller, but considering the presence of another Rio Grande endemic species, the extremely rare *Potamilus metnecktayi*, protection of this habitat is warranted as well. Part of the river segment which begins in the Big Bend National Park in Brewster County and continues to the Terrell and Val Verde County border was designated in 1978 as the National Wild and Scenic River (National Parks and Recreation Act of 1978, Public Law 95-625, November 10, 1978). This Wild and Scenic Rivers Act prohibits federal support for construction of dams, water conduits, reservoirs, or other instream activities, but does not prohibit development, levy federal control over private property, or affect existing water rights. The most important existing threats for this area, as with the Devils River population, are droughts and a decreasing water table due to ground water over-extraction. Thus, >12 m declines in the water table have been already recorded in this area (both in Hueco Bolsom and Alluvium Aquifers, El Paso and Reeves Counties, TWDB, 2014), and a 30% reduction in the existing groundwater supplies is expected by 2060 (TWDB, 2012).

Current climate model simulations suggest that the American southwest could experience a 60-year stretch of heat and drought unseen since the twelfth century (Woodhouse et al., 2010). Growing demands for water by agricultural, industrial, and recreational activities may be exacerbated by predicted climatic trends toward increased inter-annual variability in precipitation and subsequent effects on river flows (Millán et al., 2005; Milly et al., 2005). Extreme climatic events like droughts and floods are predicted to become more frequent and intense in the future (Diez et al., 2012). Freshwater fauna are particularly vulnerable to the effects of climate change because of the limited dispersal abilities of many species (Woodward et al., 2010), and the expected changes may impact freshwater ecosystems more strongly than past anthropogenic alterations (Doll & Zhang, 2010). Southern mussel populations may be particularly affected at the southern edges of their distribution, possibly due to a low tolerance to increased temperatures (Spooner et al., 2011), and also due to the low dispersal capacity to more favorable habitats located at higher latitudes or altitudes. Thus, the southernmost hydrologic regions, including the Texas Gulf, are predicted to experience 30–40% reductions in average annual discharge; and mussel extirpations, due to reductions in both discharge and loss of fish hosts, may result in losses from 15 species to 44 species (Spooner et al., 2011).

Although we found a large *P. popeii* population still existing in the Rio Grande drainage, its dramatic decline over the last century warrants immediate

species protection. Similar declines in *Margaritifera margaritifera* in Europe, despite the existence of several large remaining populations (over 120 million individuals), led to inclusion of this species in the main European policy that protects wildlife habitats and attracted most of European Community funds devoted to freshwater bivalve conservation (Geist, 2010; Gum et al., 2011; Prié, 2013; Lopes-Lima et al., accepted). Conservation plans for *P. popeii* in Texas should be aimed at promoting river management, including the prevention of water over-extraction, pollution, and maintaining flow regimes needed by the species. Since freshwater mussels are important components of aquatic ecosystems (Vaughn & Hakenkamp, 2001) and species which fulfill criteria of indicator, keystone, flagship, and umbrella species are ideal targets in aquatic conservation (Geist, 2010), protection of these areas will also help ensure protection of other Rio Grande endemics.

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