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REGULAR ARTICLE

DENSITY, APPARENT SURVIVAL, AND LOCAL POPULATION SIZE OF LOUISIANA PIGTOE (*PLEUROBEMA RIDDELLII*) IN THE NECHES RIVER, TEXAS

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ABSTRACT

Most North American unionids are imperiled to some degree, including the Louisiana Pigtoe, *Pleurobema riddellii*, which is currently under review for listing under the U.S. Endangered Species Act. Understanding a species' population dynamics, including spatial and temporal variation in survival, density, recruitment, and population size, is vital for conservation, but this information is lacking for *P. riddellii*. We conducted a mark–recapture study to estimate apparent survival, density, recruitment, and population size of *P. riddellii* within a 25-m^2 area at three sites (75 m^2 total) in the Neches River, Texas from 2014 to 2019. We used the program MARK to evaluate POPAN models for estimating population parameters. We collected a total of 392 unique individuals of *P. riddellii* over the 5-yr period and the observed recapture rate averaged 55.6%. The most parsimonious POPAN model indicated that apparent survival varied temporally, the recapture rate varied temporally and spatially, and both the entry probability (recruitment) and population size varied spatially. Apparent survival averaged 83.3% ± 3.4% (SE)/yr, overall population size across the three sites was 429 individuals (overall density = 5.7/m^2), and recruitment averaged 6.3%/yr. High survival, relatively high density, the presence of recruitment, and the lack of temporal changes in population size suggest that these populations are stable. The presence of *P. riddellii* throughout a long section of the river, including localized patches of higher abundance, suggests that the total population size in the Neches River is relatively large and the river is a global stronghold for the species.

KEY WORDS: recapture rates, mark–recapture, MARK, population dynamics, vital rates, long term

INTRODUCTION

Estimates of population vital rates and population size are important for effective species conservation (Matter et al. 2013). Vital rates, such as survival and recruitment, are the main determinants of a population's growth rate and ultimately, its viability (Akçakaya et al. 2004; Bonnot et al. 2011; Connette and Semlitsch 2015; Newton et al. 2020). Population size can influence viability primarily because small populations can be more vulnerable to Allee effects or biotic and abiotic factors (Kramer et al. 2009; Nystrand et al. 2010). Population models incorporating vital rates and population size can inform conservation efforts by making predictions about the resilience of a species to environmental impacts (Fonnesbeck and Dodd 2003; Connette and Semlitsch 2015).

North America's freshwater mussels (Unionoidae) are one of the most highly imperiled faunal groups on the continent (Williams et al. 1993; Bogan 2008; Haag 2012). Information about mussel population dynamics is especially important for evaluating population viability and responses to various environmental and anthropogenic factors. Annual survival and recruitment differ widely among mussel species, and these patterns can have a large influence on population growth and stability (e.g., Payne and Miller 2000; Villella et al. 2004; Haag 2012). However, vital rates remain unknown for numerous mussel species, and the long life span of many species requires multiyear sampling to estimate those factors (Villella et al. 2004; Newton et al. 2011, 2020). Mark–recapture studies can provide relatively unbiased estimates of

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population size and survival rates, which can be difficult to estimate directly (Daura-Jorge and Simões-Lopes 2014; Pace et al. 2017; Schachat et al. 2019).

We used a mark–recapture study to estimate apparent survival, recruitment, and population size for the Louisiana Pigtoe, *Pleurobema riddellii*, at three sites in the Neches River of eastern Texas from 2014 to 2019. This species is currently under review by the U.S. Fish and Wildlife Service (2009) for listing under the U.S. Endangered Species Act. Little life-history and population information is available for this species, and these data will be valuable to future conservation efforts.

METHODS

Study Species

Pleurobema riddellii was known historically from portions of western Louisiana, eastern Texas, and Red River tributaries in Arkansas (Vidrine 1993; Howells et al. 1996; Howells 2010, 2014). The species has experienced a large range constriction over the past decades, and sizable populations in Texas are currently known only from the upper Neches River basin (Burlakova et al. 2011; Ford et al. 2014; D. F. Ford et al. 2016). In the Neches River, *P. riddellii* occurs in riffles and shallow to moderately deep runs in stable gravel-and cobble-substrates (N. B. Ford et al. 2016; Glen 2017) and is a host specialist on drift-feeding minnows (*Pimephales vigilax*, *Cyprinella venusta*, and *Cyprinella lutrensis*; Hinkle 2018; Marshall et al. 2018). Estimates of individual growth are available for the species and maximum life span is likely over 40 yr (Ford et al. 2020). However, estimates of population vital rates and population size are lacking.

Study Area

The Neches River is a sixth-order stream and drains approximately 26,000 km^2 (Texas Parks and Wildlife Department 1974; Horizon System Corporation 2015). Seasonal stream flow patterns were similar among all years of our study (2014–2019; U.S. Geological Survey gauge 0803200 Neches River near Neches, Texas, https://waterdata.usgs.gov/tx/nwis/nwis, accessed February 10, 2021), except for the winter of 2015 and most of 2016 during which flow was consistently high ($>$30 m^3/s, maximum $=$ 134 m^3/s).

We selected three study sites that supported the highest abundance of *P. riddellii* observed over multiple years of mussel surveys in the Neches River basin (Walters et al. 2017; Ford et al. 2020). The most upstream site (HWY 79) was 8.6 km downstream of the Highway 79 bridge (Anderson County), the next site (CHC) was 22.2 km downstream of the HWY 79 site near Cherokee Hunting Club Road (Cherokee County), and the most downstream site (HWY 294) was 11.3 km downstream of CHC, upstream from the Highway 294 bridge (Cherokee County). We established a 150-m study reach at each site.

In 2014, we conducted initial site sampling by dividing each 150-m study reach into three 50-m segments and excavating 27 0.25-m^2 quadrats in each segment (total of 81 quadrats in each 150-m reach). In each 50-m segment we distributed the 27 quadrats across the stream by placing nine quadrats at randomly chosen locations in the center of the stream and nine quadrats at randomly chosen locations along each bank. We calculated an estimate of mean density of *P. riddellii* in each of the three 150-m reaches as the mean density among the 81 total quadrats (three sets of 27 quadrats per reach). In each 150-m reach, we identified the quadrat with the highest number of *P. riddellii* and established a 5 m $\times$ 5 m grid (25 m^2) centered on that quadrat for the mark–recapture study. No *P. riddellii* were collected in initial site sampling at HWY 79; we conducted a qualitative search at this site and located the 5 m $\times$ 5 m grid where the first specimen was found.

Sampling Methods

We sampled the 25-m^2 grids at each site once/yr in late summer or early fall during low-water conditions from 2014 to 2019, but we did not sample in 2018. We sampled each grid by placing a 1-m^2 quadrat at one corner of the grid, searching it for mussels by excavating the substrate, and then flipping the quadrat over to the adjacent 1-m^2 location until the entire 25-m^2 area was searched. We affixed a passive integrated transponder (PIT) tag (Biomark, Boise, ID, USA) to the shell and a numbered bee tag (Betterbee, Greenwich, NY, USA) to the opposite valve. We measured shell length of each *P. riddellii* encountered and then returned all individuals to the substrate in the grid. After 2014, we made an initial pass over the grid with a PIT tag receiver to locate previously tagged individuals and then excavated the grid as described above to ensure that all individuals were collected. On each sampling occasion, we recorded the tag numbers and measured all recaptured *P. riddellii* and tagged and measured newly encountered individuals. We also recorded dead individuals encountered in the grid. Loss of tags was rare, and no individuals lost both tags, which allowed us to identify all recaptured mussels.

Mark–Recapture Analysis

We calculated recapture rates of *P. riddellii* for each sampling event as:

$$R^c = T^r/T^m,$$

where R_c is the recapture rate for the sampling event, T_r is the number of marked *P. riddellii* recovered during the sampling event, and T_m is the total number of *P. riddellii* marked before the sampling event.

We used the POPAN model in the program MARK (White and Burnham 1999) for our mark–recapture analysis. This model has the following assumptions: (1) marks are not lost and can be read correctly, (2) sampling is instantaneous and animals are released immediately after sampling, (3) the study area remains constant and its size does not change, (4) all animals (marked and unmarked) have an equal probability of

Table 1. Densities (number/m^2) of *Pleurobema riddellii* estimated from initial site sampling and later sampling of the 25-m^2 grids at three sites in the Neches River, Texas from 2014 to 2019. Numbers in parentheses are the number of unique individuals located during each sampling event. The column "Mean" represents mean values across all 5 yr. The column "Totals" represents density estimates based on the total number of unique individuals encountered across all 5 yr and the sample area (25 m^2, or 75 m^2 for "Overall").

Site	Initial Site Sampling (2014)	25-m^2 Mark–Recapture Grid 2014	2015	2016	2017	2019	Mean	Totals
HWY 79	0.0	1.3 (32)	2.2 (54)	2.2 (54)	2.2 (56)	1.6 (40)	1.9 (47)	3.2 (79)
CHC	2.8	1.2 (29)	1.9 (48)	2.6 (65)	1.5 (37)	1.7 (42)	1.8 (44)	3.5 (87)
HWY 294	0.2	2.6 (64)	4.2 (104)	4.9 (123)	3.4 (86)	4.7 (118)	4.0 (99)	9.0 (226)
Overall	1.0	1.7 (125)	2.8 (206)	3.2 (242)	2.3 (172)	2.7 (200)	2.5 (189)	5.2 (392)

survival between each sampling event, and (5) all animals (marked and unmarked) have an equal probability of being captured between each pair of sampling events. Generally, these assumptions were met by our study. Passive integrated transponder tags may have allowed somewhat greater capture rates of previously marked individuals, but our thorough excavation of the grids likely effectively detected untagged individuals (see Discussion).

The POPAN model calculates four statistics, apparent survival (ϕ), the recapture probability during the sampling event (p), the probability of a new individual entering or being located within the sample area from the total population (entry probability, p_{ent}), and superpopulation size (N). Apparent survival is the probability of an individual surviving between sampling events, given that the organism is still present within the site, whereas the recapture probability is the probability of an individual being captured during a sampling event assuming it is alive. Entry probability (p_{ent}) is the probability of entry from the population (the population in the 25-m^2 grid) into the study area as a result of immigration or birth (i.e., recruitment). We interpreted estimates of p_{ent} derived from the POPAN model to represent annual recruitment. Adult mussels are relatively sedentary, but it is possible that some individuals moved into or out of a sampling grid. However, given the large size of the grid, this is unlikely except along the edges (Schwalb and Pusch 2007), and the number of immigrating or emigrating adults is expected to be low (Newton et al. 2015, 2020). Juveniles that recruited to a grid by dropping off host fishes initially are too small to be detected by our sampling but are detectable after about 3 yr, at which time they average >20 mm in length (Ford et al. 2020). The superpopulation size (hereafter referred to as population) is considered the number of individuals ever present in the sampling area. We calculated N for each of the three 25-m^2 grids. Both N and recruitment were rounded to the nearest whole individual. We calculated all parameters using a 1-yr time interval between successive samples, except for 2017 to 2019, where we used a 2-yr time interval to account for the lack of sampling in 2018.

We included a group effect (sampling site) and a time effect (year) in the POPAN models to evaluate spatial and temporal variation in model parameters. We used Akaike's information criterion corrected for small sample size (AIC$_c$) to rank candidate models. We used quasi-AIC$_c$ (QAIC$_c$) values to select the most parsimonious model from the list of candidate models, and we used a goodness-of-fit test in the program RELEASE in MARK to determine the fit of a chosen model. The most parsimonious model is the one with the smallest QAIC$_c$ value, which explains most of the variation in the data, while using the least number of model parameters.

RESULTS

Between 2014 and 2019 we captured a total of 392 *P. riddellii* individuals from all three sites and found eight (2.0%) dead individuals (Table 1). All dead individuals were recovered from HWY 79 in 2017 (three individuals) and 2019 (five individuals). Of the 392 *P. riddellii* individuals, we had a total of 944 captures, including 138 individuals (35.2%) that were captured once and not recaptured, 69 (17.6%) that were recaptured once (initial capture + one recapture), 94 (24.0%) that were recaptured twice, 69 (17.6%) that were recaptured three times, and 22 (5.7%) that were recaptured in all sampling events after 2014. Recapture rate averaged 55.6% across all sites and years. Recapture rates did not differ between sites (analysis of variance, $F_{9,11} = 4.26$, $P = 0.480$) but were significantly different between sampling years ($F_{12,15} = 3.49$, $P = 0.001$). Recapture rates differed only between 2016 and 2019 (Tukey honestly significant difference, $P < 0.001$). At all sites, initial captures of untagged individuals declined from 2014 to 2017, but initial captures increased in 2019 (Fig. 1). Conversely, recapture rates generally increased during the first 3 yr, then remained relatively steady after 2016, except in 2019, when recapture rates appeared to decrease substantially, particularly at HWY 294. Mean *P. riddellii* density across all three 25-m^2 grids was 1.7/m^2 in 2014 and 2.7/m^2 in 2019 (mean = 2.5/m^2; Table 1).

The most parsimonious POPAN model included apparent survival (ϕ), which varied temporally; recapture probability (p), which varied spatially and temporally; and entry probability (p_{ent}) and population size (N), which both varied spatially ($\chi^2_{(21)}$, $P = 0.002$; Table 2). Mean survival across sites was 83.3% ± 3.4% (SE). Apparent survival was >80% in all years, except between 2017 to 2019 when it was 73.8% (Table 3). Recapture probability (p) averaged 67.9% (range =

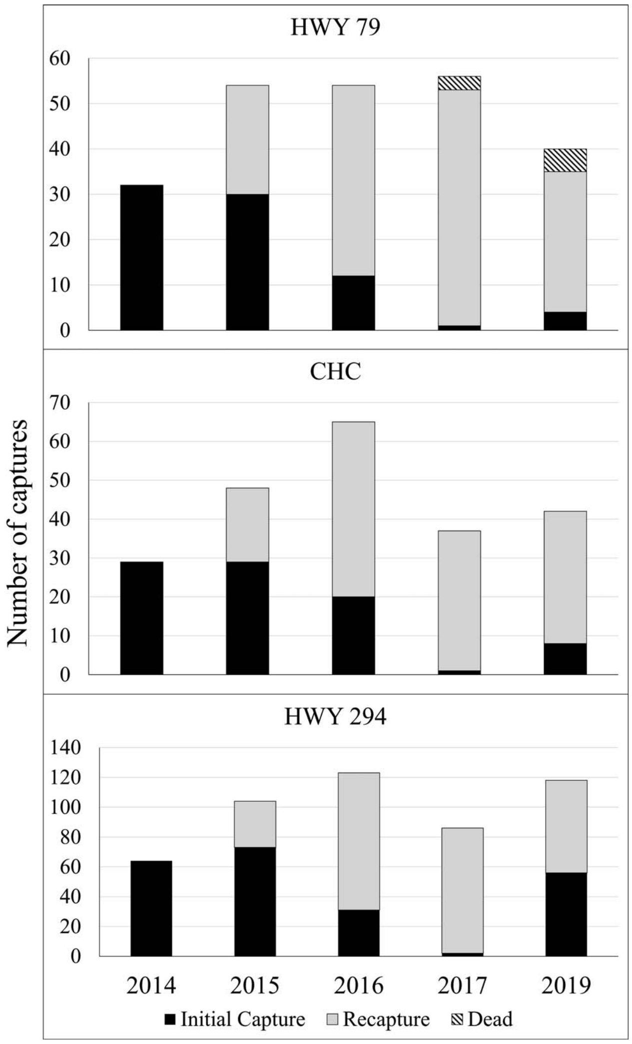

Figure 1. Captures of *Pleurobema riddellii* at three sites in the Neches River, Texas from 2014 to 2019.

38.5–95.3%) across all sites and years. Both the lowest (2015) and highest (2017) recapture probabilities were found at CHC. Recapture probability was lowest for all sites in 2015 and highest in 2017, except at HWY 79, where recapture probability was highest in 2019. Entry probability (p_{ent}) across all three sites ranged from 2.8% ± 1.4% (SE) at HWY 79 to 10.8% ± 1.3% at HWY 294 (mean across sites = 6.3% ± 1.5%). Assuming all individuals entering the populations originated from recruitment, values of p_{ent} represent the addition of 2 ± 2 (SE) to 27 ± 3 individuals/yr. The estimated total population size across all three sites was 429 ± 8 (SE) individuals (Table 3).

Of the total 79 *P. riddellii* captures at HWY 79, 14 (17.7%) individuals were captured once, 10 (12.7%) were recaptured once, 32 (40.5%) were recaptured twice, 17 (21.5%) were recaptured three times, and six (7.9%) were recaptured in all sampling events after 2014. The recapture rate at HWY 79 averaged 63.6%. We found no *P. riddelli* at HWY 79 during

Table 2. Quasi-Akaike information criterion corrected for small sample size ($QAIC_c$) ranking of POPAN models for estimating mark–recapture parameters for *Pleurobema riddellii* at three sites in the Neches River, Texas from 2014 to 2019. Model parameters are apparent survival (ϕ), recapture probability (p), probability of entry (p_{ent}), and population size (N). Parameters denoted with (t) indicate variance by survey year, (g) indicates variance by sampling site, and (.) indicates no variance by sampling time or site. Parameters that are a function of year and site simultaneously are denoted by the interaction term (g*t). NP is the number of parameters used in the model.

Model	$QAIC_c$	$QAIC_c$ Weight	NP
Φ(t) p(g*t) p_{ent}(g) N(g)	1403.565	0.506	25
Φ(g*t) p(t) p_{ent}(.) N(g)	1405.074	0.238	21
Φ(g*t) p(t) p_{ent}(g) N(t)	1405.452	0.197	21
Φ(.) p(g*t) p_{ent}(g) N(g*t)	1409.072	0.032	22
Φ(g*t) p(g*t) p_{ent}(.) N(g*t)	1410.979	0.012	31
Φ(g) p(t) p_{ent}(g) N(g)	1411.691	0.009	14
Φ(g*t) p(g*t) p_{ent}(g) N(t)	1413.145	0.004	31
Φ(t) p(t) p_{ent}(.) N(g*t)	1415.697	0.001	13
Φ(g) p(t) p_{ent}(g) N(.)	1418.395	0.000	12
Φ(g*t) p(t) p_{ent}(.) N(.)	1418.772	0.000	19
Φ(t) p(t) p_{ent}(.) N(.)	1418.909	0.000	11
Φ(.) p(g*t) p_{ent}(.) N(.)	1418.931	0.000	20

the initial site sampling in 2014. Within the 25-m^2 grid, densities were 1.3/m^2 and 1.6/m^2 in 2014 and 2019, respectively (Table 1). Entry probability was the lowest of the three sites, and an estimated 2 ± 2 (SE) new individuals immigrated to the site each year. The estimated population size at HWY 79 (87 ± 4 [SE] individuals; Table 3) was the lowest of any site.

Of the total 87 *P. riddellii* captures at CHC, 27 (31.0%) were captured once, 18 (20.7%) were recaptured once, 16 (18.4%) were recaptured twice, 20 (23.0%) were recaptured three times, and six (6.9%) were recaptured in all sampling events after 2014. The recapture rate at CHC averaged 58.1%. Density of *P. riddellii* was 2.8/m^2 during the initial site sampling in 2014 (Table 1). Within the 25-m^2 grid, densities were 1.2/m^2 in 2014 and 1.7/m^2 in 2019 (Table 1). Entry probability indicated that an estimated 5 ± 2 (SE) new individuals immigrated to the site each year. The estimated population size at CHC (96 ± 4 [SE] individuals) was similar to that of HWY 79 but much lower than that of HWY 294 (Table 3).

Of the total 226 *P. riddellii* captures at HWY 294, 97 (42.9%) were captured once, 41 (18.1%) were recaptured once, 46 (20.4%) were recaptured twice, 32 (14.2%) were recaptured three times, and 10 (4.4%) were recaptured during all sampling events after 2014. Recapture rate at HWY 294 averaged 50.5%. Density of *P. riddellii* was 0.2/m^2 during the initial site sampling. Within the 25-m^2 grid, densities were 2.6/m^2 in 2014 and 4.7/m^2 in 2019 (Table 1). Entry probability was highest at this site, and an estimated 27 ± 3 (SE) new individuals immigrated to the site each year. The estimated

Table 3. POPAN model mark–recapture parameter estimates for *Pleurobema riddellii* at three sites in the Neches River, Texas from 2014 to 2019. Parameters are apparent survival (ϕ), recapture probability (p), probability of entry into the sampling area from the overall population in the area (p_{ent}), population size (N), and recruitment (r) from the most parsimonious model (see Table 2). Error for each estimate is SE. Values of apparent survival, p_{ent}, and N are the same across sites or years, respectively, following the most parsimonious POPAN model, which indicated only temporal variation for apparent survival and only spatial variation for p_{ent} and N; the POPAN model indicated both temporal and spatial variation for p. Recruitment is the estimated number of recruits in each year and was estimated as $(p_{ent}/100) \times N$. Population size and recruitment are rounded to the nearest whole individual.

Year	Φ	p	p_{ent}	N	r
HWY 79					
2015	85.0 ± 3.7	41.3 ± 6.3	2.8 ± 1.4	87 ± 4	2 ± 2
2016	89.1 ± 2.6	74.3 ± 5.9	2.8 ± 1.4	87 ± 4	2 ± 2
2017	85.3 ± 4.3	80.3 ± 5.4	2.8 ± 1.4	87 ± 4	2 ± 2
2019	73.8 ± 3.1	88.2 ± 5.3	2.8 ± 1.4	87 ± 4	2 ± 2
CHC					
2015	85.0 ± 3.7	38.5 ± 6.7	5.4 ± 1.8	96 ± 4	5 ± 2
2016	89.1 ± 2.6	68.8 ± 6.8	5.4 ± 1.8	96 ± 4	5 ± 2
2017	85.3 ± 4.3	95.3 ± 3.2	5.4 ± 1.8	96 ± 4	5 ± 2
2019	73.8 ± 3.1	62.4 ± 7.9	5.4 ± 1.8	96 ± 4	5 ± 2
HWY 294					
2015	85.0 ± 3.7	45.9 ± 5.6	10.8 ± 1.3	246 ± 6	27 ± 3
2016	89.1 ± 2.6	74.0 ± 4.8	10.8 ± 1.3	246 ± 6	27 ± 3
2017	85.3 ± 4.3	84.6 ± 3.8	10.8 ± 1.3	246 ± 6	27 ± 3
2019	73.8 ± 3.1	61.6 ± 5.5	10.8 ± 1.3	246 ± 6	27 ± 3

population size at HWY 294 (246 ± 6 [SE] individuals) was the highest observed at any site (Table 3).

Density estimates differed substantially among sampling approaches and analytical methods. On the basis of the area of the 25-m^2 grid and estimates of population size from the POPAN model, estimated densities were 3.5/m^2 at HWY 79, 3.8/m^2 at CHC, and 9.8/m^2 at HWY 294 (overall = 5.7/m^2; see Table 3). These estimates were very similar to estimates based on area sampled and the total number of unique individuals captured across all 5 yr of sampling in the 25-m^2 grid (3.2/m^2 at HWY 79, 3.5/m^2 at CHC, 9.0.m^2 at HWY 294, 5.2/m^2 overall; Table 1). However, density estimates from quadrat sampling in individual years were about 50% lower than estimates made by the previous two methods (Table 1).

DISCUSSION

Although density and population size varied among sites, all three of our study sites in the Neches River appear to support relatively large populations of *P. riddellii*, with densities of about three to nine individuals/m^2. Other parameters suggest that these populations are stable, particularly the lack of temporal variation in population size. Survival varied across time but not by location, suggesting that annual riverwide variation in environmental factors was a more important determinant of survival than local variation among sites. However, apparent survival was generally high (usually >80%), similar to values reported for several other mussel species from stable populations (e.g., 87–>97%, Hart et al. 2001; Villela et al. 2004; Meador et al. 2011; Reátegui-Zirena et al. 2013; Wisniewski et al. 2014; Hyde et al. 2017). Values of p_{ent} were relatively low, but they represent recruitment strength similar to that seen in other stable mussel populations (e.g., 1–45%, Villella et al. 2004; Haag and Warren 2010; Matter et al. 2013); in contrast, declining populations are often characterized by a near absence of recruitment (Haag 2012).

It is important to note that our density and population size estimates for these local populations do not reflect the overall abundance of *P. riddellii* throughout the Neches River. Our estimates were obtained from small areas of high *P. riddellii* density at sites identified by previous surveys as having the highest density of the species in the river. Indeed, previous surveys at other sites in the Neches River basin found lower densities of *P. riddellii* at most sites (0.39–0.79/m^2; Andrew Glen, personal communication; Ford et al. 2014; D. F. Ford 2016). Nevertheless, the presence of *P. riddellii* throughout a long section of the river, including localized patches of higher abundance, suggests that the total population size in the Neches River is relatively large.

Variation in habitat characteristics among sites (see Ford et al. 2020) may partially explain the higher density and population size observed at HWY 294. The HWY 294 site had an extensive shallow riffle with gravel-and-cobble substrate. The CHC site had a deeper riffle with more mud and silt, and HWY 79 did not have a riffle but instead consisted of deeper, pooled habitat. *Pleurobema riddellii* is thought to prefer gravel-and-cobble substrates (Glen 2017; Ford et al. 2020), and the known hosts for *P. riddellii* are riffle-dwelling minnows (Hinkle 2018; Marshall et al. 2018). The greater abundance of riffle habitat at HWY 294 may have provided more habitat for *P. riddellii* and its host fishes.

Actual survival is difficult to estimate but is often higher than apparent survival because permanent emigration from the study area results in biased estimates of apparent survival (Gilroy et al. 2012; Hyde et al. 2017). Permanent emigration is considered less of an issue for estimating survival of mussels because of their sedentary nature (Balfour and Smock 1995; Villela et al. 2004; Newton et al. 2020), but mussels can move substantial distances in some cases (Haag 2012; Daniel and Brown 2014; Newton et al. 2015). Because we did not sample for missing *P. riddellii* outside of the mark–recapture area, we could have missed individuals that emigrated out of the 25-m^2 grid or that were displaced by the 2016 flood. Temporary emigration, such as burrowing deeper into the substrate during colder months or higher flows, also could have biased our survival estimates, but we sampled in late summer and early fall when the water was warm and the flow was low.

The use of PIT tags may have introduced some bias into our parameter estimates by increasing the likelihood of recapturing tagged individuals compared with previously uncaptured individuals (see Kurth et al. 2007). However, even by using a PIT tag reader we missed a substantial proportion of tagged individuals in any given year. This fact, combined with our extensive excavation of the substrate to find unmarked individuals, probably minimized any bias associated with the use of PIT tags.

Our estimates of density varied markedly between the initial site sampling of the 150-m reach in 2014 and later sampling of the 25-m^2 grids, even in 2014. Higher density in the 25-m^2 grids, as observed at two of the sampling sites, was expected because the areas with the highest density in the 150-m reach were selected for the sampling grids. However, our density estimates were substantially lower in the 25-m^2 grids than over the 150-m reach at CHC. The variation in density estimates between our 150-m reach and the 25-m^2 grids illustrates the characteristically patchy nature of mussel distribution (Strayer 1999; Strayer et al. 2004) and the effects of scale on sample estimates. On the basis of the results of our broader-scale initial site sampling at HWY 79 and HWY 294, *P. riddellii* might have been considered absent or rare, respectively, at those sites, but our more focused sampling of the 25-m^2 grids revealed that both sites supported substantial populations. Conversely, our initial site sampling at CHC indicated a higher density than revealed by our sampling of the 25-m^2 grids.

The large difference in density estimates between our annual samples and longer-term sampling illustrates other sample design issues. Our estimates from quadrat sampling in individual years were about 50% lower than estimates from the mark–recapture model or from the combined 5-yr quadrat sampling data set. This discrepancy is probably explained by our overall observed annual recapture rate (55.6%) and our estimate of overall recapture probability from the POPAN model (67.9%). Detectability is rarely 100%, but we appear to have missed a substantial proportion of the population in any given year despite our focused sampling in a small area and extensive excavation of the substrate. Multiyear sampling is often impractical to implement on a large scale. Our sampling methods were broadly similar to adaptive sampling, in which additional sampling effort is allocated in areas where the target species is found (Strayer and Smith 2003). A more formalized application of adaptive sampling may be appropriate when the goal of a study is to provide accurate density estimates in a single sampling effort for a patchily distributed species. In addition, accounting for detectability may help provide more accurate density estimates in single sampling events (e.g., Smith et al. 2000; Bailey et al. 2004; Wisniewski et al. 2014).

Our multiyear sampling of *P. riddellii* populations provided estimates of density, survival, population size, and recruitment that are important for conservation efforts. These estimates provide baseline data for monitoring of the species' status over time. The lack of temporal variation in population size, high survival, and apparent levels of recruitment we document suggest that these local populations are stable. Our population parameter estimates can be coupled with other demographic information to construct population models, which can provide a quantitative assessment of the current trajectory and viability of *P. riddellii* populations (e.g., increasing, stable, decreasing). The occurrence of *P. riddellii* at relatively high density throughout a long, interconnected reach of the Neches River indicates that the river is a global stronghold for this species. The decline of *P. riddellii* and other mussel species across Texas (Howells et al. 1997; Randklev et al. 2010) highlights the imperative for protection of the Neches River basin.

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