

Distribution and Demography of the Alligator Snapping Turtle (*Macrochelys temminckii*) in Texas: A 20-Year Perspective

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Abstract - Texas contains the southwestern range edge of *Macrochelys temminckii* (Alligator Snapping Turtle), but there is relatively little published information on this species within the state. To document its range and assess temporal changes in its distribution and demography, we sampled 23 sites from 1999 to 2001. We then resurveyed 22 of these sites and sampled 29 additional sites in 2020–2021. Detection outcomes were consistent between 18 of the 22 resurveyed sites. Sex ratios and body-size distributions were similar across surveys. Catch per unit effort (CPUE) was lower in areas with trotlines, corroborating known interactions between turtles and fishing gear. Patterns in CPUE indicate Gulf of Mexico-draining watersheds are important systems for the species, while CPUE was lower in Mississippi-draining watersheds.

Introduction

Macrochelys temminckii (Troost in Harlan) (Alligator Snapping Turtle) has several life-history traits that make it susceptible to human-induced population declines (Pritchard 2006). Individuals of the species take ~11–21 years to sexually mature (Dobie 1971, Moore et al. 2013, Tucker and Sloan 1997), resulting in long generation times. Juvenile survivorship is lower than that of adults (Folt et al. 2016), and consequently, high adult survivorship is required for sustained population stability (East et al. 2013, Reed et al. 2002). Disproportionately low ratios of large adults relative to other size and age classes have been documented from some locations, indicative of the persisting effects of previous commercial harvest that targeted large individuals (Howey and Dinkelacker 2013, Wagner et al. 1996). Given these life-history traits, past commercial harvest, contemporary take (both legal and illegal), and habitat alteration (e.g., impoundments) are causes of conservation concern for the species.

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Consequently, all states where this species occurs prohibit its commercial harvest and have imposed protective measures or, at minimum, recreational harvest regulations (Reed et al. 2002). Furthermore, *M. temminckii* has been considered for federal listing under the Endangered Species Act by the US Fish and Wildlife Service (USFWS) since 1982, including 2 petitions for federal listing in 1983 and 2012 (ECOS 2021). Listing has previously been denied due to lack of sufficient data (Finding on Alligator Snapping Turtle petition 1984), but a Species Status Assessment in 2021 led USFWS to propose listing the species as threatened. That assessment provided impetus to further understand the contemporary status of the turtle throughout its range, particularly in western regions, which were associated with limited monitoring data relative to other regions (ECOS 2021, USFWS 2021).

Macrochelys temminckii has been known to occur in 14 states in the southeastern United States (Reed et al. 2002). Surveys have been conducted across its range to infer large-scale distributional trends and responses to anthropogenic stressors (e.g., Boundy and Kennedy 2006, Huntzinger et al. 2019, Jensen and Birkhead 2003, Riedle et al. 2005, Shipman et al. 1995). These efforts have used historic occurrence records (Riedle et al. 2005) and harvest data (Jensen and Birkhead 2003) to infer temporal distributional trends. Surveys in states at the periphery of the geographic range of the species (Oklahoma, Kansas, Indiana, Illinois, Kentucky, and Tennessee) indicate overall range contraction based on no encounters, or encounters that were limited to restricted areas relative to historic distributions (Baxley et al. 2014, Bluett et al. 2011, Kessler et al. 2017, Riedle et al. 2008a). This pattern corroborates the hypothesis that, in general, population sizes at range peripheries tend to be relatively small, and therefore more susceptible to increased turnover rates (i.e., colonization and extinction and extirpation; Doherty et al. 2003). Baseline information provided by past records and updated with systematic surveys is critical to understand the status and range-wide responses of this cryptic species to anthropogenic influences (Howey and Dinkelacker 2013).

Given the apparent range contraction of *M. temminckii* at the northern and western peripheries of its range, its populations in Texas are particularly important to examine. This state represents the southwestern range edge of the species, where a similar pattern could be occurring. Texas ranks *M. temminckii* as an S2 (Imperiled) species of greatest conservation need, and has listed it as a threatened species since 1987, affording it legal protection from harvest within the state (species of S2 rank are considered to have a restricted range, few populations, and other characters rendering extirpation vulnerability) (Texas Parks and Wildlife 2020, Texas Register 1987). Populations in the state were previously harvested to support a commercial market in the 1960s and 1970s (Pritchard 2006). Alabama, Mississippi, and Arkansas populations were also harvested to support a commercial turtle meat market in Louisiana, presumably causing declines in these areas (Boundy and Kennedy 2006). It is plausible that after the species was protected in Texas, turtles from Texas were illegally harvested and smuggled across the state's boundary to support the Louisiana market, which ended in 2004 (Louisiana Fisheries, Sea Grant Louisiana 2004). To this day, populations in Toledo Bend Reservoir (a location of prior

commercial harvest; Pritchard 2006) and the lower Sabine River may potentially be subject to legal harvest, as these waters straddle the state border with Louisiana, where non-commercial take is still legal (1 turtle per day, per person, per vessel; Louisiana Department of Wildlife and Fisheries 2021).

Relative to other states, there is a paucity of published research on the ecology and natural history of *M. temminckii* in Texas. Most of this literature consists of distribution (e.g., Dixon 2013, Hibbitts and Hibbitts 2016, Strecker 1915) and natural history accounts (e.g., Agassiz 1857, Hay 1911, Pritchard 2006). Recent studies specific to Texas *M. temminckii* have focused on aspects of its thermal biology, habitat selection, movement, and demography (Fitzgerald and Nelson 2011; Munscher et al. 2020, 2021; Riedle et al. 2015).

A synthesis of large-scale patterns in the distribution, demography, and threats to the species throughout Texas, and longitudinal data describing the dynamics of these parameters, are lacking. To explore the spatial and temporal nature of these patterns, we conducted a large-scale survey from 1999 to 2001 within and around the purported range of *M. temminckii* in eastern Texas (Rudolph et al. 2002). From 2020 to 2021, we conducted a subsequent survey to compare with the results of the prior survey and to consolidate and expand on a foundational understanding of the distribution, demography, and threats of *M. temminckii* in Texas.

Field-site Description

We sampled reservoirs, oxbows, sloughs, river mainstems, and tributaries throughout the putative geographic range of *M. temminckii* in Texas. This area is encompassed by the watersheds of the Red, Cypress, and Sulphur rivers, which are part of the greater Mississippi River watershed, and the Sabine, Neches, Trinity, and San Jacinto rivers, which drain directly into the Gulf of Mexico (although the Sulphur and Cypress rivers are tributaries of the Red River, they are considered as separate systems here due to their disconnectedness within Texas). Based on previous research, the Trinity and San Jacinto watersheds form the western boundary of the Texas range of the species (Dixon 2013, Hibbitts and Hibbitts 2016, Munscher et al. 2021, Rudolph et al. 2002). To provide further insight into its range margin within Texas, we allocated additional survey efforts farther west of the known range within the Brazos and San Bernard watersheds.

Methods

Field surveys

We selected survey sites on the criteria of accessibility and the presumption that they consisted of *M. temminckii* habitat, including features such as low-energy pools and submerged structure that the species prefers (Harrel et al. 1996, Howey and Dinkelacker 2009, Sloan and Taylor 1987). Site visits of the initial survey occurred between April and October in 1999, 2000, and 2001. We resurveyed all sites, except for 1 creek in Newton County, in 2020 or 2021 (Table 1).

From 2020 to 2021, we extended our efforts to additional counties that contain watersheds *M. temminckii* is suspected or known to inhabit, but either lack records,

or have contradictory reports regarding its occurrence (Appendix 1; Dixon 2013, Munscher et al. 2020, Rudolph et al. 2002). In these counties, we limited the potential aquatic habitat for survey to sites that could be accessed by foot or boat and were deep enough to allow entrances of hoop traps to be submerged. We surveyed at least 1 location in each of our targeted counties from April to October 2020 and March to August 2021.

In both surveys, we deployed single-funnel, finger-throated, 4-hoop traps (hoop diameter = 1.2 m; mesh size = 2.54 cm) baited with fish. We predominantly used *Cyprinus carpio* (L.) (Common Carp) but also baited with cuts of *Ictiobus* spp., *Morone* spp., *Aplodinotus grunniens* (Rafinesque) (Freshwater Drum), and *Ictalurus* spp. to supplement Common Carp on occasion. We replaced bait daily in both surveys, as *M. temminckii* catch per unit effort (CPUE; i.e., individual turtles per trap-night) is documented to increase with the use of fresh fish (Jensen 1998). In the 1999–2001 survey, we suspended whole or large portions of fresh fish from the rear hoop. In 2020–2021, we suspended a fish-baited canister from the rear hoop of each trap. Each canister was constructed of 7.6 cm x 30.5 cm PVC pipe

Table 1. Comparison of catch per unit effort (CPUE) of *Macrochelys temminckii* between the 22 sites shared by both surveys in east Texas. Detection outcomes (i.e., presence detected or not) were the same at all but 4 sites (denoted with †). Sites marked with an asterisk (*) were conducted within the same watershed and county but in separate bodies of water. # = number of *M. temminckii* captured.

Watershed	County	1999–2001 survey			2020–2021 survey		
		#	Trap-nights	CPUE	#	Trap-nights	CPUE
Red	Fannin	0	45	0.000	0	45	0.000
	Red River	0	40	0.000	0	45	0.000
Sulphur	Titus†	0	45	0.000	1	45	0.022
Cypress	Harrison	3	30	0.100	5	45	0.111
	Harrison*	4	15	0.267	7	45	0.156
Sabine	Wood	2	45	0.044	3	45	0.067
	Wood*	4	45	0.089	12	45	0.267
	Shelby	4	45	0.089	4	45	0.089
Neches	San Augustine†	0	45	0.000	2	45	0.044
	Houston†	0	45	0.000	16	45	0.356
	Angelina/Nacogdoches	1	30	0.033	1	45	0.022
	Tyler	2	72	0.028	11	45	0.244
	Nacogdoches	5	55	0.091	15	65	0.231
	Angelina	5	45	0.111	9	45	0.200
Trinity	Liberty†	1	45	0.022	0	45	0.000
	Collin	1	45	0.022	1	45	0.022
	Anderson	3	45	0.067	17	45	0.378
	Leon	8	45	0.178	13	45	0.289
San Jacinto	San Jacinto	1	45	0.022	3	45	0.067
	Walker	2	45	0.044	2	45	0.044
Brazos	Brazos/Burleson	0	45	0.000	0	45	0.000
	Grimes/Brazos	0	45	0.000	0	45	0.000

with thirty-six 1.3-cm-diameter holes to aid in dispersal of bait scent. By preventing bait consumption, this method ensured continued scent dispersal after 1 or more turtles had entered a trap.

In both surveys, we standardized trapping efforts at most sites to 15 traps deployed for 3 consecutive nights (45 trap-nights). However, during 12 site visits, logistical constraints such as flood events and trap theft resulted in fewer trap-nights, and sampling effort exceeded 45 trap-nights during 4 site visits (Table 1, Appendix 1). We determined CPUE as the number of individual turtles per trap-night, so we did not include recapture events in its calculation (*sensu* Boundy and Kennedy 2006, Lescher et al. 2013).

In lotic systems, we set traps upstream of aquatic structure such as logjams, debris, and bank undercuts, or within pools, when available. In lentic systems, traps were placed around banks with openings facing deeper water and aquatic structure, or tied to emergent trees and other structures in open water. We checked traps approximately every 24 hours. We also documented the presence of passive fishing lines (trotlines, limblines, and juglines; hereinafter collectively referred to as trotlines).

In the 1999–2001 survey, we marked *M. temminckii* with a unique pattern of stainless-steel screws applied to the 4 posteriormost marginal scutes on the right and left sides. In the 2020–2021 survey, we marked individuals with an identifying set of notches on the marginal scutes following the North American Code (Nagle et al. 2017). On each individual, we measured straight-midline carapace length (CL; with tree calipers following Method D in Iverson and Lewis [2018]), pre-cloacal aperture tail length and total tail length (from the posterior terminus of the plastron to the vent and to the tail tip, respectively; using a flexible measuring tape), and mass (using a hanging digital scale). We grouped all turtles into 3 demographics: adult males, adult females, and juveniles of undetermined sex. We determined sex of adults based on pre-cloacal aperture tail length relative to body size and classified small individuals whose sex was ambiguous (all of which were <40 cm in CL) as juveniles. We used ranges in carapace lengths and pre-cloacal aperture tail lengths of mature individuals provided by Dobie (1971) as standards to assist sex determination. The smallest confirmed male and female were 36.0 cm and 31.5 cm in CL, respectively; these measurements are slightly smaller than the minimum sizes of sexually mature *M. temminckii* noted by Dobie (1971; males: 37 cm, females: 33 cm), and Tucker and Sloan (1997; males: 37.8 cm, females: 32.7 cm) in Louisiana.

Demography and size distribution

The limited temporal sampling effort at each site precluded meaningful site-specific demographic inferences, so we compared overall (pooled) demography from the 1999–2001 survey with that of the 2020–2021 survey to infer regional demographic trends through time. By pooling turtles from all sites, we provide a large-scale perspective of demography across the Texas range of the species. We used a chi-square goodness-of-fit test to determine differences in adult sex ratios

(adult males: females) and differences in age structure (proportion of juveniles) between the surveys.

To examine the body size distribution of *M. temminckii* through time, we constructed 2 frequency histograms of CL from turtles captured across each survey. We ensured assumptions of normality were met for each size distribution using Shapiro–Wilk tests before comparing means and variances of the 2 surveys with a *t* test and *F* test for equality of variances, respectively. We also regressed CL against mass from all turtles detected in both surveys ($n = 260$ individuals). Because the variables exhibited an exponential relationship, they were log-transformed to approximate linearity. Three turtles caught in the 1999–2001 survey were recaptured in 2020, but to maintain independence between samples, we only included the measurements from their initial capture in our analyses. However, to provide insight into the long-term growth patterns of *M. temminckii*, we report their changes in body size between the 2 surveys.

Trotline presence and CPUE

To determine differences in CPUE of *M. temminckii* between sites with and without trotlines, we conducted a chi-square goodness-of-fit test for each survey. We excluded sites with no *M. temminckii* detections from consideration to eliminate potential bias from sites where the species was absent, and organized these sites into 2 groups: those with at least 1 trotline present and those where no trotlines were observed at the time of trapping. We did not collect trotline data from 3 sites with *M. temminckii* detections surveyed in 2021, so 28 sites were considered in the 2020–2021 analysis. We made no distinction between active and abandoned trotlines, although most observed within trapped sites appeared neglected. We conducted all statistical analyses in this study using software R (version 4.0.5; R Foundation, Vienna, Austria).

Results

Geographic distribution

From 1999 to 2001, we conducted 1009 trap-nights, which resulted in 52 detections of 48 *M. temminckii* from 17 of 23 sites (Table 2). All captures occurred within the Cypress, Sabine, Neches, Trinity, and San Jacinto watersheds. We detected no individuals at the 3 sites in the Red and Sulphur watersheds, although counties within these drainages do have historic occurrence records (Dixon 2013). Our efforts at 2 sites in the Brazos watershed also resulted in no detections.

In 2020 and 2021, we conducted 2153 trap-nights at 51 sites (including 22 of the 1999–2001 survey sites). This effort resulted in 238 detections of 221 *M. temminckii* from 31 sites (Table 1, Appendix 1). An additional hand-captured individual was not considered in CPUE calculations, but was included in sex ratio and size analyses (Table 2, Appendix 1). Only 4 of the 22 sites sampled in both survey periods differed in detection outcomes (Table 1). In 2020, we failed to detect *M. temminckii* at 1 site where it was detected in 2000, and we did detect the species at 3 sites in 2020 where it was not observed during previous sampling efforts. In general, site-

specific CPUE values were much higher in the 2020–2021 survey than in previous sampling efforts, which resulted in an overall 2020–2021 survey CPUE more than twice that of the 1999–2001 survey.

Considering overall CPUE within each river watershed, the 2020–2021 survey revealed lower CPUE in the southwestern and northwestern watersheds, and higher CPUE in the central-most watersheds (Sabine and Neches). This pattern was not apparent in the prior survey, perhaps due to the lower number of captures and sites sampled (Table 3). Similar to the 1999–2001 survey, we failed to detect individuals from the Red and Brazos watersheds in 2020–2021 (Table 3). However, we did detect *M. temminckii* at 2 of 3 sites in the Sulphur watershed. We also confirmed the presence of the species in 9 counties where it was not previously documented to occur (Fig. 1; Dixon 2013, Rudolph et al. 2002). Furthermore, we received

Table 2. Trapping effort and demographic parameters of *Macrochelys temminckii* from 1999–2001 and 2020–2021. The middle column depicts 2020–2021 data from sites visited in both surveys to allow direct comparison. Adult sex ratios were similar between both surveys. Counts of individuals from each cohort are provided, with the decimal ratio in parentheses.

	1999–2001 survey	2020–2021 survey	
		Results from sites sampled in both surveys	Results from all 2020–2021 survey sites
Number of sites visited	23	22	51
Number of counties	21	20	42
Number of trap-nights	1009	1010	2153
Number of <i>M. temminckii</i>	48	122	222
Overall CPUE	0.048	0.121	0.103
Average per-site CPUE	0.054	0.119	0.108
Proportion of sites confirmed occupied	0.74	0.77	0.61
Adult females : males	21:19 (1.105)	42:41 (1.024)	86:79 (1.089)
Juveniles : adults	8:40 (0.200)	39:83 (0.470)	57:165 (0.345)

Table 3. Summary of catch per unit effort (CPUE) (*Macrochelys temminckii* individuals per trap-night) of each major watershed surveyed. A spatial pattern of progressively decreasing CPUE in watersheds to the north and southwest of the Neches and Sabine watersheds was observed in the 2020–2021 survey. This pattern was not observed during the 1999–2001 survey.

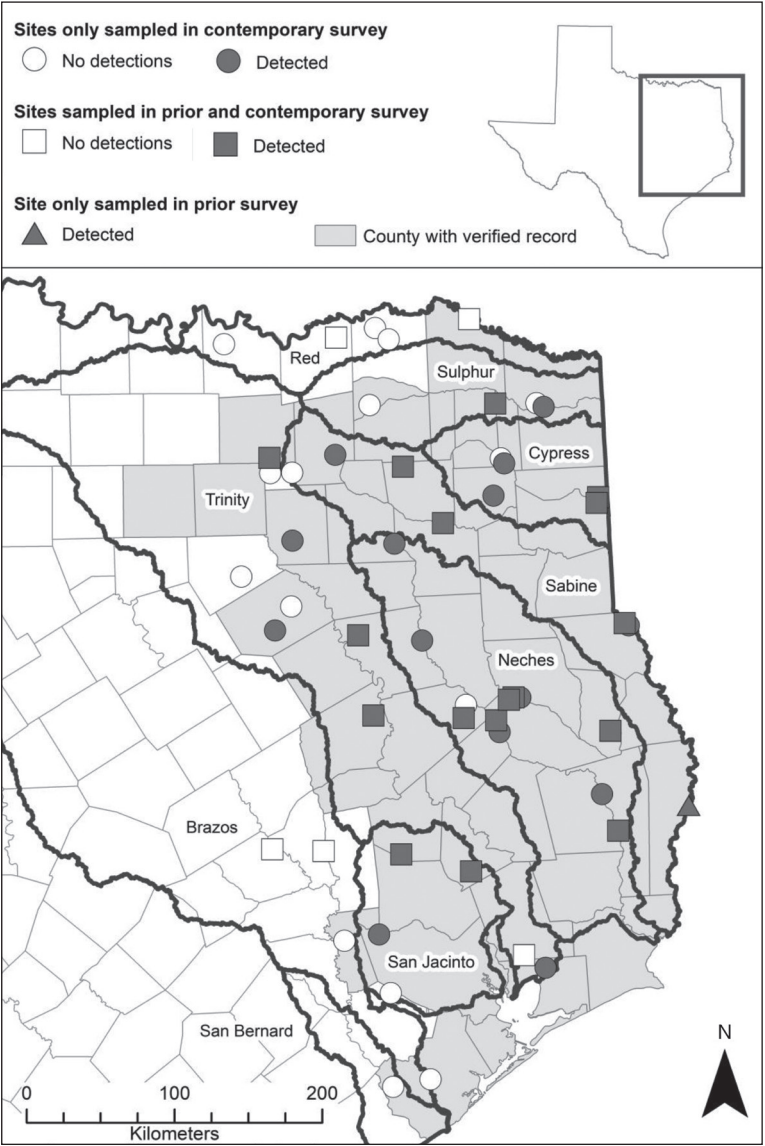
Watershed	1999–2001 survey	2020–2021 survey
Red	0.000	0.000
Sulphur	0.000	0.022
Cypress	0.156	0.071
Sabine	0.066	0.182
Neches	0.045	0.179
Trinity	0.072	0.118
San Jacinto	0.033	0.081
Brazos	0.000	0.000
San Bernard		0.000

photographs and associated locations documenting occurrences from 2 additional counties (Delta and Brazoria) where the species was not previously documented (Fig. 1, Appendix 2). The Delta County observation occurred on 14 May 2014, while an individual was observed in Brazoria County on 21 March 2019. Notably, our 2021 survey efforts in Brazoria County on the San Bernard River did not result in any captures, though we did receive photos of 2 individuals caught on trotlines supposedly from the area we trapped.

Demography and size distribution

The proportions of males, females, and juveniles were similar and not statistically different between each survey (Fig. 2). We found an even and consistent sex

Figure 1. Currently known distribution of *Macrochelys temminckii* in Texas counties, which are filled based on documented occurrences from our surveys, records in the literature, and verified citizen science reports (Appendix 2). Boundaries of major watersheds sampled are delineated with bolded lines and labeled. Detection outcomes from sites sampled in both surveys are based on 2020–2021 survey results. Most sites of no detection were along the northwestern and southwestern edges of the study area, even within watersheds (San Jacinto, Trinity, Red, and Sulphur) where the species is known to occur.



ratio of males to females in the 1999–2000 survey ($\chi^2 [1, n = 40] = 0.100, P = 0.752$) and the 2020–2021 survey ($\chi^2 [1, n = 165] = 0.297, P = 0.586$; Table 2). We observed a greater proportion (though not statistically significant) of juveniles (0.257) in the 2020–2021 survey than in the 1999–2001 (0.167) ($\chi^2 [1, n = 48] = 2.0415, P = 0.153$; Table 2).

Body size (CL) of *M. temminckii* approximated a normal distribution in both surveys ($W_{47} = 0.976, P = 0.419$ for 1999–2001 data; $W_{218} = 0.993, P = 0.358$ for 2020–2021 data), and log-transformed CL and mass pooled from both surveys were highly correlated ($r = 0.993, 95\% \text{ CI} = 0.991, 0.994$). The regression model was fitted with the coefficient 3.040 (95 % CI = 2.995, 3.084) and intercept 8.517 (95% CI = -8.682, -8.353). In the 2020–2021 survey, we captured *M. temminckii* across a greater variation in body size, but there was no significant difference in body size between the 2 surveys (mean CL: $t_{265} = 0.827, P = 0.455$; CL: $F_{218,47} = 1.374, P = 0.195$) (Table 4, Fig. 2).

Of the 3 *M. temminckii* recaptured from the 1999–2001 survey in 2020, two adult males of similar size (46.5 kg and 46.4 kg) at the time of initial capture differed drastically in growth rate. The larger male, which occupied the Cypress watershed, increased by 0.9 kg and 0.6 cm CL, while the other, which inhabited the upper Trinity watershed, grew 9.7 kg and 4.6 cm CL. A smaller female from the middle Trinity watershed initially measured at 11.0 kg exhibited the greatest change in body size, gaining 9.4 kg and 11.8 cm CL (Table 5).

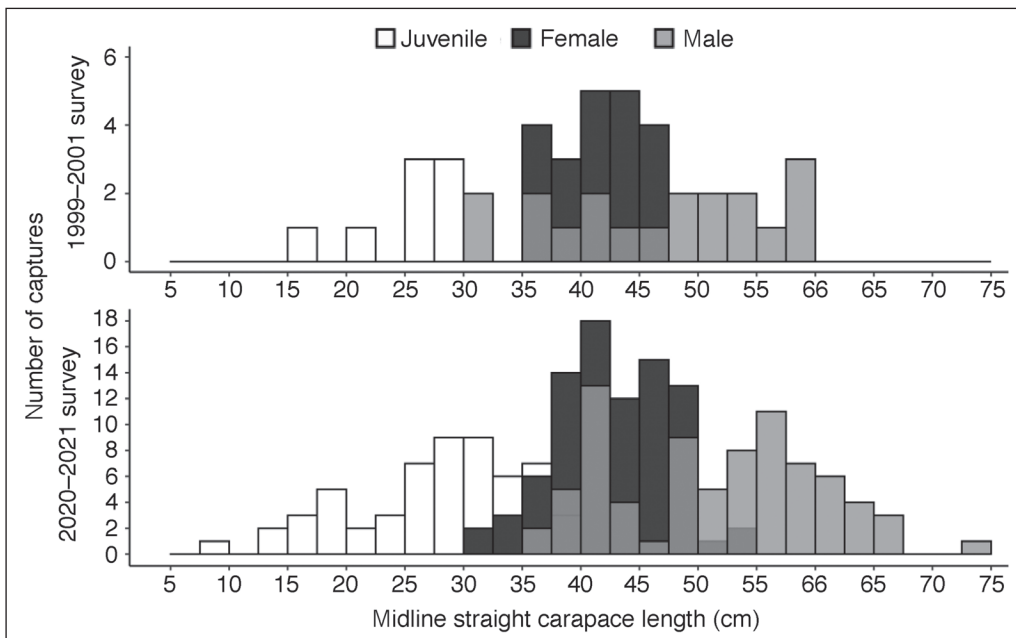


Figure 2. Body-size (straight-midline carapace length) distributions of *Macrochelys temminckii* detected in the 1999–2001 survey efforts (top; 1009 trap-nights across 23 sites) and 2020–2021 survey efforts (bottom; 2153 trap-nights across 51 sites) from east Texas. Note the range differences of the y-axes.

Trotline presence and CPUE

During 1999–2001, we captured significantly fewer *M. temminckii* where trotlines were observed (TL sites; 15 turtles captured over 347 trap-nights; CPUE = 0.043) than from sites where trotlines were not observed (NTL sites; 32 turtles over 352 trap-nights; CPUE = 0.091) ($\chi^2[1, n = 47] = 5.908, P = 0.015$). Similarly, in the 2020–2021 survey, we captured significantly fewer *M. temminckii* in TL sites (78 turtles over 585 trap-nights; CPUE = 0.133) than NTL sites (132 turtles over 658 trap-nights; CPUE = 0.200) ($\chi^2 [1, n = 210] = 8.296, P = 0.004$).

Discussion

Geographic distribution

We documented long-term persistence of *M. temminckii* in eastern Texas and expanded our knowledge of the species’ range extent, while also documenting spatial variability in CPUE. We observed that the central-eastern watersheds of the Sabine, Neches, and Trinity rivers had higher CPUE, while the peripheral northwestern and southwestern watersheds of the study area containing the Red, Sulphur, Cypress, and San Jacinto rivers had lower CPUE. In general, populations at range peripheries

Table 4. Body-size summary of *Macrochelys temminckii* documented during 1999–2001 and 2020–2021 survey efforts. Standard deviations of means are depicted in parentheses.

	Juvenile	Female	Male	All
1999–2001				
Min. CL (cm)	15.5	35.1	30.4	
Max. CL (cm)	29.0	46.1	58.3	
Mean CL (cm)	25.1 (4.7)	41.2 (3.3)	46.6 (9.2)	40.6 (9.8)
Min. mass (kg)	0.8	10.2	6.8	
Max. mass (kg)	6.0	23.8	46.5	
Mean mass (kg)	4.1 (1.8)	19.0 (4.0)	25.3 (13.5)	18.3 (11.7)
2020–2021				
Min. CL (cm)	9.0	31.5	36.0	
Max. CL (cm)	38.0	55.0	74.0	
Mean CL (cm)	28.1 (7.2)	42.8 (4.9)	51.6 (8.8)	42.1 (11.5)
Min. mass (kg)	<0.1	7.8	10.0	
Max. mass (kg)	14.9	33.4	95.8	
Mean mass (kg)	6.2 (3.6)	19.0 (6.1)	34.6 (17.5)	21.2 (15.9)

Table 5. Change in straight-midline carapace length and mass in 3 *Macrochelys temminckii* captured and measured in both the 1999–2001 and 2020–2021 surveys.

Sex	Date of first capture	Date of recapture	Time between captures	Mass (kg): initial, subsequent	CL (cm): initial, subsequent	Growth rate (cm/year)
Female	14 July 1999	13 June 2020	20 yrs, 335 days	11.0, 20.4	37.1, 48.9	0.564
Male	16 May 2001	21 July 2020	20 yrs, 66 days	46.5, 47.4	57.6, 58.2	0.031
Male	15 August 2001	1 August 2020	18 yrs, 361 days	46.4, 56.1	58.3, 62.9	0.242

are hypothesized to be prone to extirpation and increased turnover rates, which result in population distributions that are less stable than those in range interiors (Doherty et al. 2003, MacKenzie et al. 2006). If CPUE is assumed an adequate proxy of relative abundance (sensu Folt and Godwin 2013, Huntzinger et al. 2019, King et al. 2016, Lescher et al. 2013), it indicates the Sabine, Neches, and middle Trinity watersheds are important systems for the species in Texas.

The limits of the range of *M. temminckii* in Texas appear to be in the northwestern and southwestern edges of the study area, as suggested by our lack of detections from these areas, even within watersheds (i.e., the San Jacinto, Trinity, and Sulphur) where the species is known to occur. Within the state, the Red (greater Mississippi), upper Trinity, and San Jacinto watersheds may be areas with lower abundance or more patchy distribution. Sections of the San Jacinto and upper Trinity watersheds contain expansive metropolitan areas (e.g., the Dallas–Fort Worth Metroplex, Houston), and many of their tributaries have been altered by channelization and impoundments.

Buffalo Bayou, a tributary in an urbanized area of the San Jacinto watershed, supports a population of *M. temminckii* in a sinuous reach downstream from 2 major impoundments (Addicks and Barker reservoirs; Munscher et al. 2020, 2021). However, we failed to detect any individuals in a reach of this same tributary upstream of Barker Reservoir that was channelized and lacked riparian vegetation. Although the species is able to persist in urbanized areas and occurs in a variety of aquatic systems (Munscher et al. 2020), such drastically modified waterways may lack microhabitat and physical stream properties sufficient for the species (Howey and Dinkelacker 2009, Moore et al. 2013). Furthermore, the construction of Barker Reservoir could have resulted in extirpation or a decrease in abundance of an upstream population, as impoundments are posited to limit dispersal of the species (Riedle et al. 2005). In the urbanized upper Trinity watershed, Tarrant County contains the westernmost Texas locality for the species (Iverson and Hudson 2005). However, east (i.e., downstream) of this site, our surveys suggest *M. temminckii* occurs sporadically, where a network of impoundments and other anthropogenic alterations may prevent a uniform pattern of occurrence. It is also plausible that the relatively arid climate of this region provides lower quality habitat for *M. temminckii* (Thompson et al. 2016).

While the upper Texas coastal plain is predicted to meet the climatic requirements for *M. temminckii* (Thompson et al. 2016), the occurrence of the species in the San Bernard River was unexpected given the lack of records from the Brazos watershed to the east. This low-elevation, poorly draining coastal region is prone to frequent flood events (Ray et al. 2011), which could displace turtles from source populations of the San Jacinto watershed and lead them to disperse to westward coastal tributaries (e.g., Armand Bayou) and waters of the Brazos and San Bernard watersheds (sensu Jones and Sievert 2009). Introduction by humans, either accidental or purposeful, could also explain occurrences in the Brazos watershed and the San Bernard River. For example, a *M. temminckii* was found at the Texas A&M Aquaculture Facility in the Brazos watershed in the late 1990s. Because it was

found on land far west of the known range of the species, the animal was presumed to have been released from captivity (D. Gatlin, Texas A&M University, pers. comm.; Rudolph et al. 2002). If the San Bernard *M. temminckii* were introduced without human aid, the sporadic occurrence of individuals in the coastal Brazos watershed and small coastal tributaries is plausible, as well as a more likely destination (relative to the San Bernard farther west) for individuals originating from the San Jacinto watershed. The restricted overland dispersal ability of *M. temminckii* is likely the limiting factor to its occupancy of these coastal waters. Regardless of the dispersal mechanism, individuals from the San Bernard likely either represent a small or a nonviable population in which individuals are too sparsely distributed to detect with our methods.

Consistency in detection outcomes for 18 of the 22 sites sampled in both surveys suggests occupancy of *M. temminckii* has remained generally stable over the past 2 decades. The 4 sites with different detection outcomes between surveys may indicate a true change in site presence, changes in detectability, or random chance during the trapping occasions. Detection is influenced by environmental variables, survey methods, and population density (Buchanan et al. 2019, Tanadini and Schmidt 2011). The low numbers of *M. temminckii* ($n = 1$ to 3 individuals) detected in 2020–2021 at the sites where they were not previously found may indicate individuals have occurred there in low numbers. Sampling efforts in 2020 at the only site where *M. temminckii* (1 individual) was detected in the 1999–2001 survey and not in the 2020–2021 survey resulted in many of our traps being damaged by *Alligator mississippiensis* (Daudin) (American Alligator), which may have lowered captured probability of *M. temminckii*. Regardless, only 2 trapping occasions separated by 20 years do not allow us to draw firm conclusions about non-detections. However, the general pattern of persistent occupancy and documented presence at additional sites provides important knowledge of the distribution of *M. temminckii* in Texas.

The greater than twofold increase in overall CPUE from the 1999–2001 survey to the 2020–2021 survey was likely driven by factors affecting trapping success, such as a higher abundance of *M. temminckii* during the recent sampling period. However, we consider it unlikely that populations have increased at these sites to the degree that would account for the increase in CPUE. Populations of long-lived species like *M. temminckii* increase slowly without immigration (Congdon et al. 1994). We are not aware of major habitat changes within any of the twice-surveyed sites that might favor immigration of *M. temminckii* into the areas. Most of the turtles we captured across the 22 shared sites were adults, and would have been alive before 1999 (Trauth et al. 2016). Thus, we consider differences in trapping methods to be the most likely explanation for increased CPUE in 2020–2021. It could be that by preventing bait consumption, PVC bait canisters increased the potential for multiple *M. temminckii* to enter the same trap.

The overall CPUE in 2020–2021 was one-half that reported from surveys across the state of Arkansas (CPUE = 0.234; Wagner et al. 1996) and from northeastern Arkansas (CPUE = 0.278; Trauth et al. 1998), which suggests the species is less

abundant in Texas. In contrast, the 2020–2021 CPUE was higher than what has been documented from Oklahoma (CPUE = 0.058; Riedle et al. 2005), southwestern Louisiana (CPUE = 0.019; Huntzinger et al. 2019), and southeastern Louisiana (CPUE = 0.057; Boundy and Kennedy 2006), which may suggest that the species is more abundant in Texas than in these states. However, inferences from cross-study comparisons in CPUE should be made with caution because CPUE may be calculated to include or exclude recapture events (Folt and Godwin 2013, Lescher et al. 2003), and environmental and survey method variation may also influence CPUE. For example, Wagner et al. (1996) deployed 6 traps for 1 night per site, and visited 300 locations in Arkansas. This led to a large area sampled with fewer trap-nights, relative to our survey. By spreading effort among many sites in this manner, there is a greater opportunity to encounter turtles from a greater number of populations, while the effect of an unoccupied site on CPUE is relatively small. Furthermore, deploying more than enough traps to detect the turtles occupying an area can lead to a lower CPUE than if fewer traps are set (Boundy and Kennedy 2006). This scenario plausibly explains the pattern of larger than typical CPUEs from 2 of our sites where 5 instead of 15 traps were deployed. Boundy and Kennedy (2006) usually deployed 25 traps for 1 night per site, which may have contributed to the lower CPUE reported in that study. Huntzinger et al. (2019) deployed fewer traps per site than we did, although allocated 3 nights per site, perhaps granting more comparability with our survey. Trap saturation (e.g., inter-trap distance) within trapped waters is yet another variable that can confound CPUE comparisons. Decreasing saturation can decrease detectability of *M. temminckii* (D. Rosenbaum et al., unpubl. data) and thus is likely an important source of variation across surveys and sites. Spacing of traps is not usually reported from *M. temminckii* surveys (but see Trauth et al. 1998), nor is it usually standardized within surveys. Instead, it is determined by the availability of microhabitat inferred to be favorable for capture (e.g., Baxley et al. 2014, Huntzinger et al. 2019, Shipman and Riedle 2008). Differences in trapping protocols and variability in trap saturation make it difficult to interpret differences in capture data among studies, and highlight that CPUE does not necessarily translate well to abundance without accounting for other sources of variation. It is important to report sampling and trapping protocols and complete results so that cross-study comparisons may be more informative.

Range contraction of *M. temminckii* is evident throughout Oklahoma (Riedle et al. 2005), but has not been documented in Texas. In Oklahoma, the species has been recorded from as far west as the Washita River (Wickham 1922), but recent surveys have only documented it as far west as the Muddy Boggy River (M. Howery, Oklahoma Department of Wildlife Conservation, pers. comm.), which meets the Red River ~60 km to the east of the Washita River. However, we failed to detect *M. temminckii* along similar longitudes of the Red River watershed to the Muddy Boggy River in Texas (Lamar County). Reintroduction efforts of *M. temminckii* to the Washita watershed have recently taken place (Moore et al. 2013), and could potentially facilitate dispersal through the Red River watershed in both states. We also observed that average CPUE in Texas watersheds decreased with increased

proximity to Oklahoma, suggesting there may be smaller population sizes in Red River-draining watersheds of Texas and Oklahoma.

With the exception of 1 site sampled in 2000, we did not survey the border region of the lower Sabine watershed, so are unable to comment on the distribution of *M. temminckii* throughout this area. Huntzinger et al. (2019) failed to trap any individuals from 3 Louisiana sites adjacent to the Texas border, and only documented 1 juvenile drowned on a passive fishing line, which suggests relative abundance in the lower Sabine may be low. Pritchard (2006) reported that Louisiana hunters traveled to the Texas side of the Sabine River to catch *M. temminckii* in 1981. More recently, poachers were prosecuted in 2016 for violating the Lacey Act by regularly harvesting *M. temminckii* from Texas waters and transporting them to Louisiana to support their business (Eastern District of Texas 2017). These cases imply that incentives to hunt in Texas (i.e., higher catch) are driven by the perception that *M. temminckii* is more abundant in Texas. Several fishermen confided to us that they came to Texas from Louisiana to trap *M. temminckii* because the species is less frequently encountered in Louisiana. Such perceptions and statements should be interpreted cautiously, as local anecdotes regarding the species have not always been accurate (Boundy and Kennedy 2006, Trauth et al. 1998).

Demography and size distribution

Based on the distribution of size classes and proportions of each sex, results from both surveys indicate an even population structure with stable sex ratios over a 20-year timespan. Similar sex ratios and mean body sizes for *M. temminckii* have been reported from Louisiana, Georgia, Oklahoma, and Arkansas (Boundy and Kennedy 2006; Jensen and Birkhead 2003; Riedle et al 2005, 2008b; Trauth et al. 1998). Some surveys have reported uneven sex ratios (Folt and Godwin 2013, Howey and Dinkelacker 2013, Trauth et al. 2016). Female-biased ratios are proposed to reflect historical harvest pressure due to the targeting of larger and more profitable cohorts that predominantly consist of males (Folt and Godwin 2013, Howey and Dinkelacker 2013, Lescher et al 2013). The equal sex ratios we observed do not reflect a history of selective harvest, assuming that demography of unharvested *M. temminckii* populations is similar to that of unharvested *Chelydra serpentina* (L.) (Common Snapping Turtle) populations, which usually exhibit equal sex ratios (Howey and Dinkelacker 2013).

Due to higher mortality in younger cohorts, freshwater turtle populations have been generalized to consist of ~30% juveniles (Bury 1979, Howey and Dinkelacker 2013). However, juvenile proportions from *M. temminckii* surveys vary widely, from 0.633 in northeastern Arkansas (Trauth et al. 1998) to 0.200 in Georgia (Jensen and Birkhead 2003; see Boundy and Kennedy [2006] for a cross-survey compilation of juvenile proportions). We observed a relatively low proportion of juveniles in both the 1999–2001 survey (0.167) and 2020–2021 survey (0.257). This variation could result from habitat differences as well as demographic differences (e.g., annual survivorship). Trapping in deeper bodies of water may bias adult detection, whereas surveys allocated to smaller tributaries may favor capture of juveniles (East et al. 2013, Luhring et al. 2016, Moore et al. 2013, Riedle et al. 2008b). A

greater proportion of juveniles may indicate higher recruitment and survivorship of young cohorts or, on the contrary, can also result from increased adult mortality (Lescher et al. 2013). Exemplifying the latter case, the high proportion of juveniles and lower numbers of adults reported from northeastern Arkansas were sampled from a historically harvested area, and are consistent with the impact of size-biased harvest activities (Trauth et al. 1998). Similar effects of previous harvest pressure were not evident from our study area, as we observed higher adult proportions and a normal size distribution of individuals in both surveys. The lower proportion of juveniles we observed may be attributable to limited recruitment, or lower juvenile survivorship. In *C. serpentina*, for example, annual juvenile survivorship is documented to be lower than that of adult females (Congdon et al. 1994). While lower *M. temminckii* juvenile survivorship may be underlying our observed patterns, extensive mark–recapture surveys are needed to confirm the causal mechanism.

The large difference in growth between the 2 recaptured males attests to the multiple intrinsic factors (e.g., metabolism, activity) and extrinsic factors (e.g., food availability, water temperature) that affect growth (Dobie 1971). The greater growth in the smaller female may be explained by the increased growth rate of younger (i.e., smaller) turtles (Dobie 1971). Mean annual CL growth reported from subadults in Louisiana was higher than annual growth rates we observed, although the rate of the female and 1 male fall within the range of subadult measures (Harrel et al. 1997). Our observations are also consistent with growth patterns reported from 22 individuals recaptured between 1996 and 2015 in Arkansas (Trauth et al. 2016). Turtles in this population exhibited similar variability in growth, as well as increased growth rate of smaller individuals.

Trotline presence and CPUE

Across both surveys, we observed a lower relative abundance of *M. temminckii* at sites with trotlines and other passive fishing gear. Capture and drowning of turtles on lines is well documented (Barko et al. 2004, Glorioso et al. 2020, Huntzinger et al. 2019, Moore et al. 2013, Sloan and Taylor 1987, Steen and Robinson 2017). Furthermore, a 1% increase in annual mortality of adult female *M. temminckii* has been modeled to result in population declines (Reed et al. 2002), so a potential mechanism of the negative relationship is well understood. Negative response to fishing pressure could be an indirect association mediated by increased human presence, as well. It is plausible that increased human activity in an area raises the probability of encounters with turtles, some of which result in persecution of *M. temminckii* (Burger and Garber 1995, Moore et al. 2013).

Conservation implications

Our survey efforts have provided 2 cross-sectional views of the status of *M. temminckii* in Texas, and provided detailed documentation of the southwestern edge of its geographic range. Sites that were resurveyed confirmed that occupancy and demography of *M. temminckii* within these areas remained generally stable over the past 2 decades. Higher CPUE than in Oklahoma and Louisiana may attest to benefits of more stringent protection of the species in Texas (Texas Register 1987).

Lower CPUE in areas experiencing fishing pressure would seem to corroborate deleterious effects of passive fishing equipment on turtle populations. A clear resulting implication for conservation is that management strategies to reduce incidental mortality from fishing should be a priority. The lower CPUE documented from sites in the Mississippi River watershed, and apparent absence of the species from western areas of the Red River watershed, is cause for concern if the Texas range has contracted concomitantly with the Oklahoma range.

Future long-term sampling efforts at specific sites could produce data necessary to refine understanding of the species' demography, life history, and population dynamics (East et al. 2013, Folt et al. 2016). Periodic monitoring at set temporal intervals across large spatial scales will help build a longitudinal dataset to infer dynamics of occupancy and population persistence (King et al. 2016, Lescher et al. 2013). Because of the slow growth and maturation and long generation time of *M. temminckii*, long-term monitoring is vital to detect demographic responses to and recovery from perturbances.

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Appendix 1. Catch per unit effort (CPUE) of *Macrochelys temminckii* for all sites sampled in 1999–2001 and 2020–2021 survey efforts, as well as overall counts and averages for each watershed with at least 1 detection. # = number of *M. temminckii* captured.

Watershed	County	1999–2001 survey			2020–2021 survey		
		#	Trap-nights	CPUE	#	Trap-nights	CPUE
Red	Grayson				0	45	0.000
	Lamar				0	41	0.000
	Lamar				0	18	0.000
	Fannin	0	45	0.000	0	45	0.000
	Red River	0	40	0.000	0	45	0.000
Overall		0	45	0.000	0	194	0.000
Mean per-site		0	42.5	0.000	0	38.8	0.000
Sulphur	Bowie				0	45	0.000
	Cass				3	45	0.067
	Delta				0	45	0.000
	Titus	0	45	0.000	1	45	0.022
Overall		0	45	0.000	4	180	0.022
Mean per-site		0	45	0.000	1.0	45.0	0.022
Cypress	Camp				0	45	0.000
	Camp				2	45	0.044
	Upshur				2	45	0.044
	Harrison	3	30	0.100	5	45	0.111
	Harrison	4	15	0.267	7	45	0.156
Overall		7	45	0.156	16	225	0.071
Mean per-site		3.5	22.5	0.183	3.2	45.0	0.071
Sabine	Hunt				16	45	0.356
	Rockwall				0	4	0.000
	Shelby				4	30	0.133
	Newton	2	47	0.043	0	0	NA
	Shelby	4	45	0.089	4	45	0.089
	Wood	2	45	0.044	3	45	0.067
	Wood	4	45	0.089	12	45	0.267
Overall		12	182	0.066	39	214	0.182
Mean per-site		3.0	45.5	0.066	5.6	30.6	0.152
Neches	Cherokee				15	45	0.333
	Houston				0	45	0.000
	Jasper				5	45	0.111
	Nacogdoches				11	15	0.733
	Trinity				7*	45	0.156
	Van Zandt				3	45	0.067
	Angelina	5	45	0.111	9	45	0.200
	Angelina/Nacogdoches	1	30	0.033	1	45	0.022
	Houston	0	45	0.000	16	45	0.356

Watershed	County	1999–2001 survey			2020–2021 survey		
		#	Trap-nights	CPUE	#	Trap-nights	CPUE
Overall	Nacogdoches	5	55	0.091	15	65	0.231
	San Augustine	0	45	0.000	2	45	0.044
	Tyler	2	72	0.028	11	45	0.244
		13	292	0.045	95	530	0.179
	Mean per-site	2.2	48.7	0.044	7.9	44.2	0.210
Trinity	Chambers				11	45	0.244
	Ellis				0	45	0.000
	Kaufman				1	45	0.022
	Navarro				0	43	0.000
	Navarro				10	45	0.222
	Rockwall				0	45	0.000
	Anderson	3	45	0.067	17	45	0.378
	Collin	1	45	0.022	1	45	0.022
	Leon	8	45	0.178	13	45	0.289
	Liberty	1	45	0.022	0	45	0.000
	Overall	13	180	0.072	53	448	0.118
	Mean per-site	3.3	45.0	0.072	5.3	44.8	0.118
San Jacinto	Fort Bend				0	45	0.000
	Waller/Harris				9	38	0.237
	San Jacinto	1	45	0.022	3	45	0.067
	Walker	2	45	0.044	2	45	0.044
	Overall	3	90	0.033	14	173	0.081
	Mean per-site	1.5	45.0	0.033	3.5	43.3	0.087
Brazos	Brazoria				0	45	0.000
	Waller				0	9	0.000
	Brazos/Burleson	0	45	0.000	0	45	0.000
	Grimes/Brazos	0	45	0.000	0	45	0.000
	Overall	0	90	0.000	0	144	0.000
	Mean per-site	0	45.0	0.000	0	36.0	0.000
San Bernard	Brazoria				0	45	0.000
Survey-wide sum		48	1009	0.048	221	2153	0.103
Survey-wide mean (SD)		2.087 (2.130)	43.870 (9.951)	0.054 (0.066)	4.093 (5.397)	44.166 (11.523)	0.108 (0.147)

*An 8th individual at this site was captured by hand, so was not considered in CPUE calculation.

Appendix 2. Sources compiled on the distribution of *Macrochelys temminckii* in Texas. Photograph voucher numbers for records filed at Texas A&M University Biodiversity Research and Teaching Collections are provided for records first published herein.

County	Citation	County	Citation
Anderson	Raun and Gehlbach 1972	Madison	Prestridge 2021
Angelina	Rudolph et al. 2002	Marion	Prestridge 2021
Bowie	Huse 2020	Montgomery	Munscher et al. 2019
Brazoria	Present study (TCWC-PV025)	Morris	Dixon 2013
Camp	Present study, Baxter-Bray et al. 2021	Nacogdoches	Collins et al. 2000
Cass	Present study (TCWC-PV026)	Navarro	Present study (TCWC-PV031)
Chambers	Present study (TCWC-PV027)	Newton	Guidry 1953
Cherokee	Dixon 2013	Orange	Guidry 1953
Collin	Rudolph et al. 2002	Panola	Dixon 2013
Dallas	Franklin et al. 2021	Polk	Rakowitz et al. 1983
Delta	Present study (TCWC-PV028); H. Crenshaw, 14 May 2014 Texas Parks and Wildlife, pers. comm.	Rains	Dixon 2013
Franklin	Franklin and Catalán 2009	Red River	Dixon 2013
Freestone	Dixon 2013	Rusk	Dixon 2013
Galveston	Norrid et al. 2021	Sabine	Rudolph et al. 2002
Gregg	Dixon 2013	San Augustine	Present study (TCWC-PV032)
Hardin	Raun and Gehlbach 1972	San Jacinto	Rudolph et al. 2002
Harris	Raun and Gehlbach 1972	Shelby	Raun and Gehlbach 1972
Harrison	Dixon 2013	Smith	Raun and Gehlbach 1972
Henderson	Strecker 1926	Tarrant	Iverson and Hudson 2005
Hopkins	Dixon 2013	Titus	Dixon 2013
Houston	Dixon 2013	Trinity	Present study (TCWC-PV033)
Hunt	Present study (TCWC-PV029)	Tyler	Dundee 1995
Jasper	Rudolph et al. 2002	Upshur	Present study (TCWC-PV034)
Jefferson	Guidry 1953	Van Zandt	Present study (TCWC-PV035)
Kaufman	Present study (TCWC-PV030)	Walker	Raun and Gehlbach 1972
Leon	Rudolph et al. 2002	Waller	Present study (TCWC-PV036)
Liberty	Strecker 1915	Wood	Raun and Gehlbach 1972