Ocean and Coastal Management 155 (2018) 8–14

Contents lists available at ScienceDirect

Ocean and Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

Considering diamond-backed terrapin (*Malaclemys terrapin*) nesting habitat and reproductive productivity in the restoration of Gulf of Mexico coastal ecosystems

Steven H. Pearson*, Jon J. Wiebe

Louisiana Department of Wildlife and Fisheries, 646 Cajundome Boulevard, Lafayette, LA 70503, USA

ABSTRACT

Diamond-backed terrapins (*Malaclemys terrapin*) are coastally distributed between south central Texas in the Gulf of Mexico along the Gulf and Atlantic Coast north through Massachusetts. Throughout their range many different biotic and abiotic factors have been shown to influence terrapin abundance, distribution and nesting success. Louisiana Department of Wildlife and Fisheries (LDWF) implemented a multi-year (2013–2015) project which evaluated diamond-backed terrapin nesting ecology along Louisiana's coastline, principally within the Deltaic Plain. We focused on identifying nest site locations, nest predators and predation rates, nest surface characteristics, nest depth, clutch size, egg morphometrics, nest and nest survivorship. Our results indicate that terrapin nesting occurs coast-wide in locations where suitable nesting substrates exist. Nests are laid in open areas and beneath dense vegetative cover with surface slopes in all orientations. Depredation rates range between 50 and 100 percent depending on nesting beach location. Intact clutch size averages 6.5 eggs and varies between one and 15 eggs. Statewide, average egg morphometrics are: mass 10.6 g, length 36.9 mm and width 23.6 mm. Average nest ceiling depth is 7.7 cm and average nest floor depth is 11.8 cm. Seventy-six percent of all nests surveyed were fully or partially depredated. In 2015 we studied in detail 92 nests from a single nesting site; 49% of nests hatched at least 1 egg, 43% of eggs were depredated, 31% of the eggs hatched and 26% had unknown fate. We provide Louisiana's first evaluation of diamond-backed terrapin nesting ecology critical for determining the conservation status of diamond-backed terrapins within Louisiana. Our findings provide natural resource managers with critical life history information that can be incorporated into current and future coastal restoration plans to benefit diamond-backed terrapins.

1. Introduction

Globally, accelerated coastal land loss continues to threaten the sustainable management of coastal wildlife communities and the species that rely on its services. Louisiana exemplifies this issue as described in the most recent iteration of the state's coastal master plan (Coastal Protection and Restoration Authority, 2017). Extreme rates of coastal land loss continues to be documented in association with a variety of historic and temporal threats (e.g. levee construction, oil and gas canals/saltwater intrusion, global warming, subsidence, oil spills, etc.) (Day et al., 2000; LOSCO, 2010; Cowan et al., 2014). Further, coastally distributed species such as the diamond-backed terrapin (*Malaclemys terrapin*), continue to demonstrate population declines in association with these and additional threats (e.g. historic and active commercial/recreational fisheries, shifting climate regimes) which have the potential to synergistically interact, thereby accelerating these deleterious impacts to the broader coastal community (Hay, 1917; Day et al., 2000, 2007; Anderson and Alford, 2014; Osland et al., 2016). Therefore, it is imperative that targeted species information (e.g. habitat requirements, reproductive parameters) be collected and incorporated within the broader restorative landscape goals (e.g. reduction of storm impacts, commerce enhancement, etc.) to ensure the needs of impacted coastally distributed species like the diamond-backed terrapin are more effectively addressed.

Diamond-backed terrapins (*Malaclemys terrapin*) are small emydid turtles that inhabit coastal brackish waters along the Atlantic coast between Massachusetts and the Florida Keys, and along the Gulf Coast from Florida to Texas (Ernst and Lovich, 2009). Significant declines in terrapin populations have been documented throughout the species' range and are associated with a host of factors including habitat loss, global climate change, and anthropogenic caused mortalities (Hay, 1917; Tucker et al., 2001; Sheridan et al., 2010; Anderson and Alford,

* Corresponding author.
E-mail addresses: stevenhpearson@gmail.com (S.H. Pearson), jwiebe@wlf.la.gov (J.J. Wiebe).

https://doi.org/10.1016/j.ocecoaman.2018.01.017
Received 6 July 2017; Received in revised form 12 January 2018; Accepted 15 January 2018
0964-5691/

Table 1
Coastal and tidal shoreline for United States Gulf Coast states. Louisiana (in bold) represents the largest expanse of potential diamond-backed terrapin habitat of all Gulf Coast states (NOAA Office for Coastal Management, 2016). We found most nesting sites along the coastal shoreline but note that nesting occurs in tidal shoreline areas where nesting substrate exists.

State	Coastal Shoreline Length (km)	Tidal Shoreline Length (km)
Florida (Gulf)	1239	8199
Alabama	85	977
Mississippi	71	577
Louisiana	**639**	**12,426**
Texas	591	5406

2014). Louisiana represents the largest expanse of potential diamond-backed terrapin habitat within the Gulf of Mexico (GOM) (Table 1) yet knowledge of the species within state waters has been characterized as a “black hole” (Roosenburg, 2008). To responsibly address regional diamond-backed terrapin population declines, a comprehensive understanding of population dynamics (e.g. abundance, distribution, and reproductive productivity) is required. In Louisiana, the Louisiana Department of Wildlife and Fisheries (LDWF) has been working to close this data gap, and recently provided an introductory evaluation of terrapin abundance and distribution throughout the state's coastal zone (Pearson and Wiebe, 2014; Selman et al., 2014). Concurrently, with these studies, LDWF initiated an evaluation of terrapin reproductive biology specifically focusing on defining nesting localities, and determining regional reproductive ecology. Collectively these components are considered essential in assessing diamond-backed-terrapins recuperative ability to recover from historical losses and respond to contemporary threats (identified or otherwise) within regional and coast-wide scales. Further, these and related data will be instrumental in supporting Louisiana's terrapin population restoration in concert with the state's ongoing and expansive coastal restoration activities.

Diamond-backed terrapin nesting has been described within several populations along the length of the species range with, latitudinal and environmental driven differences being noted in life history traits (Seigel, 1980a, 1984). However, aside from a single citation (Burns and Williams 1972) and incidental observations, there has been limited information of terrapin reproductive biology throughout coastal Louisiana. Recent observations suggest that terrapins within Louisiana are seasonally active with brumation occurring between November and February. Further, nesting activities as determined by capture of gravid females and/or observation of excavated nests occur between May and July while post-nesting activity such as egg incubation, hatching and adult foraging continues into November. However, select female life history traits (e.g. age or size at first reproduction, nesting frequency, clutch size, egg size, hatching success and longevity) may potentially vary within Louisiana and across the terrapin's geographic range. Here we present terrapin nesting ecology and reproductive productivity data (2013-15) from Louisiana's coastal management basins within the deltaic plain and highlight an intensive evaluation within a single, large nesting beach (hereafter 2015 study site). Specific endpoints of interest include 1) Delineation of terrapin nesting habitats throughout coastal Louisiana 2) Documentation of diamond-backed terrapin reproductive productivity metrics (e.g., nest depredation, fecundity, egg morphometrics, hatchability and hatchling emergence) and 3) Identification of terrapin nest and beach section characteristics (e.g., GPS position, nest age, nest elevation, slope of nest and vegetative presence) throughout coastal Louisiana. Collectively these data demonstrate the species' preferential nesting habitat requirements as well as data on reproductive potential. These data are critical components required to support the incorporation of diamondback-terrapin nesting habitat within Louisiana's broad-scale coastal restoration projects.

2. Methods

2.1. A Priori delineation of potential nesting habitat

Potential nesting habitat was defined as coastal habitat above the high tide line that was open or lightly vegetated, sandy or shell beach, adjacent to open water and within zones of brackish or saline marsh (Burger and Montevecchi, 1975; Feinberg and Burke, 2003). Prior to nest searching attempts, potential terrapin nesting habitats were identified utilizing terrapin capture locations and the most recent Google Earth® aerial imagery.

2.2. Nesting habitat searching

In 2013 terrapin nesting sites were surveyed on barrier island beaches within the Barataria basin during the months of June and July (Fig. 1). In 2014, we utilized pre-selected geographic locations delineated in Google Earth® to implement diamond-backed terrapin nesting searches during the months of June, July and August within the Barataria, Pontchartrain and Terrebonne basins (Fig. 1). If additional nesting locations (i.e., not pre-selected in Google Earth®) were identified in the field, they were also searched. We searched for terrapin nests by walking beaches and investigating potential nest sites. Potential nest sites were found using signs such as female tracks, indentations in the substrate, turned substrate and presence of predated eggs at the surface.

2.3. Reproductive productivity

Upon locating a nest, we assessed presence of nest predators using visual observation, track identification and remote camera. We assessed nest predation rates on a basin and coast-wide level. Clutch size was determined by excavating intact and depredated nests and by counting clusters of depredated eggs. Eggs within intact nests were removed from the nest cavity, measured and then returned and recovered once the full nest had been documented. Intact egg length and width were measured

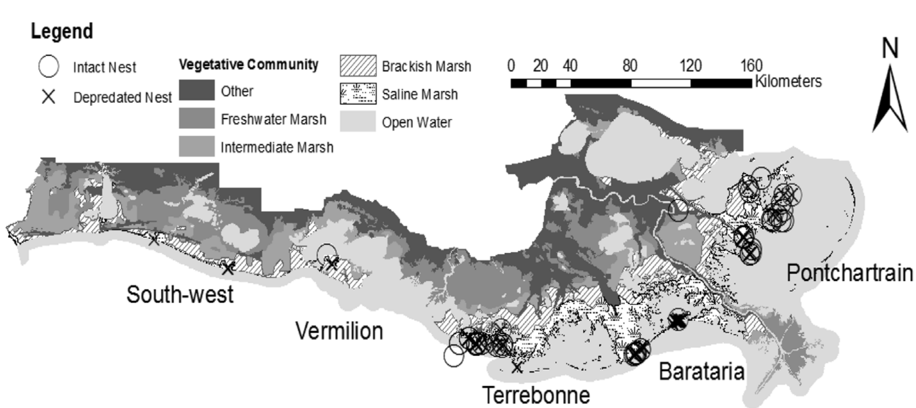

Fig. 1. Nest sites documented across Louisiana's coast between 2012 and 2015. We surveyed hard beach habitats in saline and brackish marsh for signs of terrapin nesting. The bulk of our work was performed in Ponchartrain, Barataria and Terrebonne Basins and nests were documented in the South-west and Vermillion management Basins. The 2015 study site was in southwestern Terrebonne Basin.

to the nearest 0.1 mm with Mitutoyo digital calipers (model CD-6″CS) and mass was determined with an Ohaus® scale (model PS 251) to 0.1 g ± 0.1 g. We measured nest depth (mm) to the first/last eggs laid, nest surface orientation and percent vegetative cover, and determined nest survivorship and egg hatching success by following the fate of intact nests throughout the nesting season.

2.4. Hatchling size

Hatchling turtles were opportunistically collected by hand while completing nest surveys and while excavating nests. Hatchling straight-line carapace length, straight-line plastron length, and plastron width at the posterior end of the bridge were measured to the nearest 1 mm ± 0.5 mm with tree calipers and mass was determined with an Ohaus® scale (model PS 251) to 0.1 g ± 0.1 g. Hatchlings were released at the capture site and on occasion were hydrated with fresh water before release.

2.5. 2015 nesting beach surveys

During the 2015 survey period, we selected a single nesting beach for intensive study to refine initial reproductive productivity estimates.

2.6. 2015 reproductive productivity

Utilizing the methods described above, intact and depredated terrapin nests were identified and documented within the study location. Of these, a subset (n = 20) of intact nests were assigned to two treatment groups: protected (n = 10) and unprotected (n = 10). “Protected” constitutes nests covered by galvanized wire fencing (mesh size 5 × 10 cm) to deter mammalian predators and limit predation but large enough to allow hatchling turtles through. “Unprotected” constituted no protective covering (i.e. natural conditions). All nests were monitored weekly when weather conditions permitted throughout incubation to document individual nest success.

2.7. Nesting habitat surveys

Habitat surveys were implemented within designated reaches (n = 3) of the study beach, with each reach having heavy terrapin use compared to other areas of the beach. Within each section, vegetation surveys were implemented along established line transects at 10 m spacing which ran perpendicular to the water's edge from the most recent high tide line to the back barrier marsh. Transects ranged between 5 and 20 meter in length. Each transect had designated sampling plots (1-meter radius circle) spaced every 2 m. Vegetation surveys within each plot consisted of determining each plant species present, maximum height of each plant species, number of stems present of each species (abundance) and percent coverage for each species. Additionally, beach surface characteristics were documented including slope and surface orientation. Collectively, these data were utilized to calculate the following individual vegetative species metrics in the R package ‘BiodiversityR’ (Kindt and Coe, 2005).

Frequency is the number of plots where a specific plant was present (*p*) out of the total number of plots observed.

Relative frequency is the ratio of a plant species' frequency to the total sum of all plant species' frequency. The quotient is the percent frequency of a particular plant.

Density is the number of stems (**count**) of a single species counted within the circular plots divided by the summed area of surveyed plots.

Relative Density is a percentage that describes the number of stems per area of a single species in relation to the total number of stems of all species counted within the area of the surveyed plots.

Percent Cover is the coverage provided by each plant species within a sample plot. In this survey, percent coverage by plant species within each circular plot was estimated by two to three biologists.

Relative Percent Cover is the percent a plant species covers the plot in relation to the sum of the total coverage of all plant species.

Importance Value is the sum of relative density, relative frequency, and relative dominance of plants within a defined area. This summative value describes an organism's importance within a community (Curtis and McIntosh, 1951). A plant can score between 0 (least important) and 300 (most important) relative to the other plants recorded in a community.

3. Results

3.1. Delineation of nesting habitat and associated searches

In 2013, terrapin nesting beaches were delineated within the Barataria management basin in which 78 nests were documented (Fig. 1). Abbreviated nest searching was also performed within the Pontchartrain management basin but failed to document nesting activity. Concurrently, adult diamond-backed terrapins and potential nesting locations were documented within select regions of the Pontchartrain Basin.

In 2014, terrapin nesting beaches were delineated within the Pontchartrain, Barataria and Terrebonne management basins, resulting in 174 documented nests (Fig. 1). During these surveys a beach with high terrapin nest densities was identified (i.e., 2015 Study Site).

3.2. Reproductive productivity

3.2.1. Nest predators

Nest predators documented at depredated nest sites included ants, birds (corvids and gulls), coyotes (*Canis latrans*), ghost crabs (*Ocypode quadrata*), otters (*Lutra canadensis*) and raccoons (*Procyon lotor*).

3.2.2. Nest predation rates

During 2013, 78 nests (11 intact and 67 depredated; 86% depredation rate) were documented within Barataria management basin.

During 2014, 174 nests (44 intact or hatched and 129 depredated; 75% depredation rate) were documented within the Pontchartrain, Barataria and Terrebonne management basins (Table 2).

During 2015, 92 nests (49 intact or hatched and 43 depredated) were documented within the 2015 Study Site. The observed depredation rate was 47%.

3.3. Clutch size

In 2013, average clutch size from all nests (N = 78) was 5.9 eggs, average clutch size from intact nests (n = 11) was 7.9 eggs and depredated nests (N = 67) were 5.6 eggs. In 2014, average clutch size from all nests (N = 174) was 5.2 eggs, average clutch size from intact nests (n = 44) was 5.9 eggs and depredated nests (N = 129) were 5.0 eggs. In 2015, average clutch size from all nests (N = 92) was 5.2 eggs, average clutch size from intact nests (N = 49) was 6.6 eggs and depredated nests (N = 43) were 5.1 eggs (Table 3). Clutch size ranged between one and fifteen eggs (Table 3).

Table 2
Nesting search results within select basins.

Basin	Nest Total	Intact Nests	Depredated Nests	Depredation Rate
Pontchartrain	45	14	31	68%
Barataria	98	12	86	88%
Terrebonne	109	26	82	75%
2015 Study Site	92	49	43	47%

Table 3
Average clutch size for depredated and intact nests.

Basin	Depredated Nests	Intact Nests
Pontchartrain (N = 45)	4.3 (N = 30, SD = 2.9, Range 1–10)	5.9 (N = 15, SD = 2.9, Range 1–12)
Barataria (N = 98)	5.3 (N = 87, SD = 2.6, Range 1–11)	7.2 (N = 11, SD = 2.9, Range 1–12)
Terrebonne (N = 109)	5.3 (N = 82, SD = 2.9, Range 1–13)	6.5 (N = 26, SD = 1.8, Range 1–10)
2015 Site (N = 108)	5.1 (N = 45, SD = 2.8, Range 1–12)	6.6 (N = 63, SD = 3.4, Range 1–15)

Table 4
Average egg morphometrics from each basin.

Basin	Egg Length (mm)	Egg Width (mm)	Egg Mass (mm)
Pontchartrain (N = 27)	37.2 (SD = 2.6)	23.9 (SD = 1.6)	ND
Barataria (N = 48)	36.9 (SD = 2.1)	23.0 (SD = 0.7)	11.8 (SD = 2.5)
Terrebonne (N = 34)	37.5 (SD = 1.6)	24.1 (SD = 2.7)	ND
2015 Study Site (N = 144)	36.0 (SD = 2.5)	23.1 (SD = 1.9)	9.9 (SD = 1.9)

3.4. *Egg size*

In 2013, egg length averaged 36.9 mm (N = 48, SD = 2.1, max = 42.8 mm, min = 32.3 mm). Egg width averaged 23.0 mm (N = 48, SD = 0.7, max = 24.3 mm, min = 21.5 mm). Egg mass averaged 11.8 grams (N = 48, SD = 2.5, max = 13.2 g, min = 4.2 g) (Table 4).

In 2014, egg length averaged 38.6 mm (N = 62 SD = 2.1, max = 51.0, min = 31.0) within the three management basins studied. Egg width averaged 24.8 mm (N = 62, SD = 2.3, max = 33.7, min = 17.0). Egg mass was not reliably measured in 2014 and is not reported.

In 2015, egg length averaged 36.0 mm (N = 142, SD = 2.5, max = 42.0.0, min = 31.0). Egg width averaged 23.1 mm (N = 142, SD = 1.9, max = 28.0, min = 19.0). Egg mass averaged 9.9 grams (N = 107, SD = 1.9, max = 14.5 g, min = 5.7 g).

3.5. *Nest success*

Forty-nine of the 92 nests documented at the 2015 Study Site were intact. Of the 10 protected nests 8 nests were not depredated. Predation of protected nests likely occurred by coyotes. Of the 10 Un-protected nests, 6 nests were not depredated. In total 14 nests (8 protected and 6 unprotected) containing 109 eggs produced 82 hatchlings for a cumulative nest success rate of 75%. Inter-clutch variation in nest success between the 14 nests, ranged from 36% to 100%. All nests successfully produced hatchlings.

3.6. *Hatchling sizes*

In 2015 (N = 31), hatched terrapin carapace length averaged 31.4 mm (N = 31, SD = 2.9, max = 38.0 mm, min = 26.0 mm). Carapace width averaged 25.0 mm (N = 31, SD = 3.4, max = 30.0 mm, min = 16.0 mm). Carapace height averaged 16.1 mm (N = 31, SD = 2.2, max = 26.0 mm, min = 13.0 mm). Plastron length averaged 26.3 mm (N = 31, SD = 4.9, max = 32.0 mm, min = 10.0 mm). Plastron width averaged 15.5 mm (N = 31, SD = 1.6, max = 18.0 mm, min = 12.0 mm). Hatchling mass averaged 7.88 grams (N = 30, SD = 1.6, max = 10.3 g, min = 4.5 g).

Table 5
Average nest depth from each basin and from the 2015 Study Site.

Basin	Depth to Nest Top	Depth to Nest Floor	Principal Nesting Substrate
Pontchartrain	9.4	13.9	Shell Hash
Barataria	5.4	9.1	Sand
Terrebonne	7.8	11.4	Shell Hash
2015 Study Site	10.9	14.6	Shell Hash

3.7. *Nest characteristics*

3.7.1. *Nest depth*

In 2013, the average depth to the last deposited eggs (i.e. top of nest chamber) was 4.7 cm and the average depth to the nest floor was 9.4 cm. 2013 nests were located on sand beaches in the Barataria Basin. In 2014, the average depth to the last deposited eggs (i.e. top of nest chamber) was 8.3 cm and the average depth to the nest floor was 12.1 cm. In 2015, the average depth to the last deposited eggs was 10.9 cm and the average depth to the nest floor was 14.6 cm. 2014 nests were primarily located on shell hash beaches in the Ponchartrain and Terrebonne Basins (Table 5).

3.8. *Nest surface characteristics*

In 2013, vegetative cover of nests varied between 0% and 90%. Thirty-seven of 78 nests had no vegetative cover and 62 of 78 nests had 50% or less vegetative cover. Nest slope varied and ranged between 0° (i.e. a nest on flat ground above the beach slope) and 21° (e.g. a nest on a rising beach) (Table 6). Of nests not on flat ground (N = 55), 38% of nests were oriented on north facing slopes, 24% on south facing slopes, 14% on east facing slopes and 24% on west facing slopes (Table 7).

In 2014, vegetative cover of nests varied between 0% and 60%. One hundred and thirty-three of 174 nests had no vegetative cover and 173 of 174 nests had 50% or less vegetative cover. Nest slope ranged between 0° (e.g. a nest on flat ground above the beach slope) and 24° (e.g. a nest on a rising beach) (Table 6). Of nests not on flat ground (N = 112), 14% of nests were oriented on north facing slopes, 25% on south facing slopes, 22.5% of nests located on east and 38.5% of nests were on west facing slopes (see Table 7).

In 2015, vegetative cover of nests varied between 0% and 100%. Thirty-eight of 92 nests had no vegetative cover and 56 of 92 nests had 50% or less vegetative cover. Nest slope ranged between 0° (e.g. a nest on flat ground above the beach slope) and 20° (e.g. a nest on a rising beach) (Table 6). Of nests not on flat ground (N = 67), 79% of nests were oriented on north facing slopes, 11% on south facing slopes, 6% of nests located on east and 4% of nests were on west facing slopes (Table 7).

3.9. *Nesting beach characteristics*

Nesting beaches were predominantly open areas consisting of less than 20% percent vegetative cover (Table 8). The dominant nesting substrate in Barataria Basin was sand while shell hash was dominant in

Table 6
Nest surface characteristics from each basin over the full study for nest not on bare or flat ground. Vegetative cover in all basins ranged between 0 and 100%. Minimum nest slopes within each basin was 0.

Basin	Vegetative Cover: Avg.	Nest Slope: Avg	Nest Slope: Max.
Pontchartrain	38.0	7.5	24
Barataria	61.7	8.6	21
Terrebonne	ND	4.7	20
2015 Study Site	44.9	5.9	20

Table 7
Nest orientation from each basin over the full study period. Nests represented are those not found on flat land (n = 234).

Basin	Total Nests	% Nest Oriented to North	% Nest Oriented to East	% Nest Oriented to South	% Nest Oriented to West
Pontchartrain	41	5	76	9.5	9.5
Barataria	55	38	14	24	24
Terrebonne	71	17	6	26.5	50.5
2015 Study Site	67	79	6	11	4

Table 8
Beach surface characteristics describing the three beach sections (reaches) studied along the 2015 nesting beach. In all reaches the tallest plant species was *Iva frutescens.*

Reach	Length (m)	Area (m^2)	Maximum Plant Height (m)	Mean Percent Cover	
				Vegetation	Bare Ground
1	49.2	658.0	1.5	18	82
2	45.7	542.32	1.8	18	82
3	52.9	2004.82	1.5	9	91

Pontchartrain and Terrebonne Basin (Table 5). Maximum vegetative height within the nesting beach was 1.8 m (Table 9). The most commonly encountered plant genera were *Chamaesyce*, *Oenothera*, *Ipomoea*, *Sesbania*, *Solidago*, *Iva*, and *Distichlis* (Table 9).

4. Discussion

Diamond-backed terrapins are an important part of the coastal ecosystem. Terrapins are a broadly distributed species that may persist in the environment through conditions that cause mortality of other species (e.g. fish kills from low dissolved oxygen) and the decline of other potential bio-indicator species and thus may be a useful bio-indicator species with which to monitor coastal ecosystem health. As mulluscavores, terrapins control *Littorina* spp. (i.e. snails) and in turn prevent the snails from grazing *Spartina alterniflora* to the marsh platform, thus have been considered a keystone species (Silliman and Bertness, 2002).

Declines in terrapin populations have been associated with multiple threats throughout the species' range (Butler et al., 2006). Much of this decline has been attributed to historic overharvesting paired with more temporal threats such as pervasive habitat loss, bycatch associated with commercial fisheries, and geographically-expansive stochastic events (e.g., hurricanes, oil spills) (Butler et al., 2006). In Louisiana, contemporary threats to terrapins are anthropogenic caused mortalities from derelict fishing gear (Anderson and Alford, 2014), oil spills that occur throughout the state's coastal zone (e.g. Deepwater Horizon) and habitat loss through natural and anthropogenically accelerated causes (e.g. subsidence, channelization). Within Louisiana, a coast-wide terrapin distribution and abundance evaluation suggested population irregularities (e.g., reduced relative abundance, altered population dynamics) which may be driven by regional and localized threats within select management basins (Pearson and Wiebe, 2014). A better understanding of terrapin nesting ecology and reproductive ecology (e.g., nesting beaches distribution, nest density, fecundity and hatchability) within each management basin can inform a broader ecosystem approach to coastal restoration (e.g., enhancing restoration projects with terrapin nesting habitat). The diamond-backed terrapin life history data presented here provides additional evidence that enhancing project designs and refining existing projects can increase the ecological productivity of restoration projects and have greater impacts in successfully restoring Gulf of Mexico natural resources and ecosystem function.

4.1. Diamond-backed terrapin reproductive ecology

The life history data described above provides additional evidence that differences in clutch size among regional terrapin populations does exist. The hypothesis is that as latitude decreases, clutch size decreases and egg size increases (Zimmerman, 1989; Ernst and Lovich, 2009; Allman et al., 2012). Allman et al. (2012) found that clutch sizes in Rhode Island, Maryland and South Carolina were 16.1, 12.2 and 6.0, respectively. This trend in decreasing clutch size with latitude is apparent when published literature across the range are compared (Seigel, 1980a; Roosenburg and Dunham, 1997; Feinberg and Burke, 2003; Roosenburg et al., 2014). Zimmerman (1989) compared across the latitudinal gradient and found significant differences occurring between the New Jersey and South Carolina but only minor differences between South Carolina and Florida. Similar to Zimmerman (1989) and Allman et al. (2012) the data presented here indicate that average clutch sizes

Table 9
Vegetative species found within the nesting study areas including its associated importance value, frequency, density, dominance, and the relative frequency, density, and dominance values of each.

Species	Importance Value	Frequency	Density	Dominance	Relative Frequency	Relative Density	Relative Dominance
Chamaesyce sp.	65.8	0.5	1857.0	1105.0	16.5	34.5	14.8
Oenothera lacinata	43.5	0.4	1240.0	592.0	12.6	23.0	8.0
Ipomoea sp.	28.2	0.5	5.0	961.0	15.2	0.1	12.9
Sesbania sp. *#2*	27.7	0.4	336.0	597.0	13.5	6.2	8.0
Solidago sempervirens	27.6	0.2	611.0	783.0	5.7	11.3	10.5
Iva frutescens	22.2	0.2	173.0	973.0	5.9	3.2	13.1
Distichlis spicata	21.5	0.1	533.0	669.0	2.6	9.9	9.0
Lippia nodiflora	12.4	0.1	0.0	702.0	3.0	0.0	9.4
Spartina patens	9.4	0.0	250.0	270.0	1.1	4.6	3.6
Borrichia frutescens	9.2	0.1	112.0	217.0	4.3	2.1	2.9
Sesuvium sp.	6.5	0.1	55.0	163.0	3.3	1.0	2.2
Bare Ground	6.1	0.2	0.0	0.0	6.1	0.0	0.0
Spartina alterniflora	5.5	0.1	102.0	131.0	1.8	1.9	1.8
Sesbania sp. *#1*	4.9	0.1	32.0	49.0	3.7	0.6	0.7
Lespidium virginicum	3.4	0.1	54.0	55.0	1.7	1.0	0.7
Baccharis halimifolia	1.7	0.0	21.0	42.0	0.7	0.4	0.6
Unknown 4	1.6	0.0	6.0	25.0	1.1	0.1	0.3
Sporobolus virginicus	1.0	0.0	2.0	42.0	0.4	0.0	0.6
Cuscuta sp.	0.9	0.0	0.0	50.0	0.2	0.0	0.7
Salicornia virginica	0.7	0.0	0.0	14.0	0.6	0.0	0.2
Unknown	0.2	0.0	1.0	2.0	0.2	0.0	0.0

were smaller than those found in northern populations and within the range of southern populations (see Seigel, 1980b; Butler, 2000). Egg morphometrics (Table 3) were larger in Louisiana than in Rhode Island, New Jersey and Maryland but were similar to those from South Carolina and Florida (Zimmerman, 1989; Allman et al., 2012). In Louisiana, clutch sizes of intact nests within each management basin averaged between 5.9 and 7.2 eggs per nest (Table 3).

Differences in observed fecundity between Louisiana and other terrapin populations within northern latitudes may have broader implications towards terrapin recovery after natural (e.g. hurricanes) or anthropogenic perturbations (e.g. overfishing, oil and gas spills) if concurrent evolution of other life history parameters has not occurred. Life history parameters that could evolve alongside shifts in clutch size that may offset reduced clutch size are nest survivorship, hatchling survivorship, age of first reproduction, clutch number per year and reproductive longevity. However, there are no data to suggest that any of these life history parameters have concurrently evolved in such a way that would offset population recovery times. Allman et al. (2012) suggest that the shift in clutch size/egg size are likely related to embryonic energetics as the nesting female invests more in individual eggs. In the absence of nest and hatchling predation this increased investment in individual eggs may increase egg and nest survivorship which could in turn impact long term population growth. However, nest and hatchling predation in Louisiana occur at similar rates as those reported across the range (Table 2) (Roosenburg and Place, 1994; Feinberg and Burke, 2003), minimalizing any increases in survivorship. If the number of clutches laid per year is greater in Louisiana that in other regions then this may be a mechanism by which terrapin populations could recover more rapidly. There is no reason to believe that shifts in other life history parameters have occurred although additional research is needed to confirm this assertion. If no concurrent shifts in other life history parameters have occurred, the recruitment rate and population growth of Louisiana terrapins will be retarded beyond those of more highly fecund populations. In a changing landscape with ever increasing anthropogenic impacts, recovery of diamond-backed terrapin populations with low fecundity will be difficult.

In Louisiana, terrapin nesting habitats are concentrated at the outer fringes of the marsh, on barrier islands, and at lower densities within interior marshes. Within the interior marshes the transition between the broad low lying marsh platform and water is typically a sharp escarpment with no nesting substrate. The nesting substrate and surface characteristics of available nesting areas may play an important role in determining a nests' success. Barataria basin is the only region with a sandy beach substrate which likely was the reason for the shallower nests laid within this basin. Sand beaches are more compact than shell beaches which may lead to terrapins digging shallower nest in these habitats. Although few nests were found on dredge material within Louisiana we hypothesize that if terrapins adopt dredge spoil sites as nesting substrate that the nests would be shallower than those found on shell beaches.

Fifty percent of all nests found were not found on bare ground even though during our survey describing the 2015 study site we found that greater than 80% of the nesting beach was characterized as bare ground. This disparity between the amount of bare ground and the percentage of nest found under vegetation suggest that many terrapins select shaded areas to nest. The selection of shaded/vegetated areas to nest may impact nest survival or hatchling sexes by impacting the nest temperature. The plant with the highest importance on the 2015 nesting beaches was a *Chamaesyce* sp. which has a deep tap root and often develop a broad canopy which casts shade. Nesting beneath this plant should produce cooler nests which could improve survivorship for nest and influence the sex ratio produced by the beach. However, selecting vegetated areas can also be detrimental to nest success as roots can grow through the nest cavity and cause nest failure (Lazell and Auger, 1981; Butler et al., 2004). Additionally, we found that beach micro-topography may be a factor in nest site selection, with many nests being laid in locations oriented to the North or East. If micro-topography is indeed a factor in terrapin nesting, it may influence nest success, as beach areas with Northern or Eastern exposures are not as directly heated by the sun through a day, which could create similarly cool microclimates inside a nest as those influenced by shade.

4.2. Restoration potential

Nesting substrates across Louisiana include sandy beaches and large grained shell hash. Dredge material may also act as a nesting substrate in Louisiana as has been utilized for nesting elsewhere in the terrapin's range (Wnek et al., 2013). Natural nesting substrates (i.e. sand and shell hash) are limited in Louisiana's Deltaic Plain with sandy nesting beaches occurring only on barrier islands while shell hash typically occurs at the outer fringes of the saline marsh and in spotty locations along marsh edges within interior marshes. Within the Chenier Plain sandy beaches are more abundant. Dredge spoil is present along many of the canals that have fragmented Louisiana marshes but have not been found to support terrapin nesting. Within Louisiana's marshes, nesting habitats are relatively rare and likely act as limited resources across Louisiana's Deltaic Plain. Many female terrapins may be required to make seasonal migrations that as long as 30 km to find suitable nesting habitat. Many of the restoration projects being proposed and planned within Louisiana occur within this zone and may be beneficial to terrapin populations if built with terrapin friendly features such as artificial nesting habitat, access points and elevated dredge spoil banks. Elevated restoration enhancements for terrapin nesting should be $\geq$ 0.5 m above the mean high tide line after accounting for estimated relative sea level rise, at least 10 m wide and $\geq$ 10 m long.

Across much of Louisiana's coastline, ongoing marsh recession has created wide bays between intact large swaths of saline marsh and the barrier islands. These open bays likely act as barriers to continued nesting on the barrier islands within these two management basins. However, we have documented low rates of terrapin nesting along barrier islands in the Terrebonne management basin which suggest that if marsh habitat can be restored behind barrier islands, self-sustaining terrapin populations could be re-established. In the Barataria management basin the barrier islands maintain large intact marshes with high densities of terrapins that nest along the barrier islands. As coastal barrier island restoration projects are designed the creation of large back barrier tidal marsh habitat should be considered within the project design.

Since 2010, Louisiana has made great strides in describing terrapin populations, nesting ecology and interactions with crab fisheries. These efforts have helped determine that terrapin populations exist in Louisiana and that nesting successfully occurs across the coastline, but that current threats to terrapin populations are largely caused by anthropogenic activities such as land development, commercial fishing and oil spills. The data presented here are helpful to define several Louisiana specific life history parameters that can be utilized to better model how terrapin populations may change moving forward into the future. The data presented here provides a strong initial understanding of terrapin nesting ecology in Louisiana and it is imperative that terrapin research continue across the Louisiana coastline to further define terrapin life history parameters and to determine how terrapins respond the different restoration projects.

Funding

This work was supported by the State Wildlife Grant T-107 managed by the Louisiana Department of Wildlife and Fisheries.

Author contributions

JW conceived of the work, SP&JW designed and implemented surveys, SP analyzed the data, SP & JW wrote and edited the manuscript and both approve of the submitted version.

Acknowledgements

Due to both the expansive nature of the Louisiana coastline and secretive nature of our species of interest, we would like acknowledge the extensive efforts of program personnel for their dedication and hard work in facilitating this effort: Charlie Wahl, James Ialeggio, Ariel Dauzart, Sergio Merino, Cody Haynes, Casey Wright, Wade Hardy, Todd Credeur, Will Selman, Aerial White, Ben Stultz, Matt Weigel, Dane Cassady, Amy Magro, and Rob Dobbs. Authors greatly appreciate public and private coastal landowners (Conoco Phillips Corporation, Edward Wisner Donation, LDWF Office of Fisheries, Delacroix Corporation, Terre Aux Boeuf Land Company as well as Biloxi Marsh Lands Corporation and Lake Eugenie Land and Development Corporation) for without their collaboration we would have been unable to implement this project. Further, we would like to recognize our funding sources (State Wildlife Grant SWG-T-107 and supplementary funding from LDWF). Thanks to colleagues within the Department's Natural Heritage Program (Beau Gregory) as well as Louisiana Department of Environmental Quality (David Greenwood, Eric Garner, Guy LeFleur) and Coastal Protection and Restoration Authority (Todd Folse) for their continued support and collaboration. Additionally, during 2015 the following volunteers were extremely helpful in documenting terrapin nesting at the 2015 Study Site, Nicole Finger (University of Louisiana, Lafayette), Jordan Donini (Southeastern University), Kalli Trahan (Comeaux High School) and Maggie Cunningham.

References

Allman, P.E., Place, A.R., Roosenberg, W.M., 2012. Geographic variation in egg size and lipid provisioning in the diamondback terrapin *Malaclemys terrapin*. Physiol. Zool. 85, 442–449.

Anderson, J.A., Alford, A.B., 2014. Ghost fishing activity in derelict blue crab traps in Louisiana. Mar. Pollut. Bull. 79, 261–267.

Burger, J., Montevecchi, W.A.T., 1975. Nest site selection in the terrapin Malaclemys terr*apin*. Copeia 1975, 113–119.

Burns, T.A., Broadhurst, K.L., 1972. Notes on the reproductive habits of *Malaclemys terrapin pileata*. J. Herpetol. 6, 237–238.

Butler, J.A., 2000. The status and distribution of the Carolina diamondback terrapin, Malaclemys terrapin centrata. In: Duval Co. (Ed.), Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

Butler, J.A., Broadhurst, C., Green, M., Mullin, Z., 2004. Nesting, nest predation and hatchling emergence of the Carolina diamondback terrapin, *Malaclemys terrapin centrata*, in northeastern Florida. Am. Midl. Nat. 152, 145–155.

Butler, J.A., Heinrich, G.L., Seigel, R.A., 2006. Third workshop on the ecology, status, and conservation of diamondback terrapins (*Malaclemys terrapin*): results and recommendations. Chelonian Conserv. Biol. 5, 331–334.

Coastal Protection and Restoration Authority, 2017. In: Coastal Master Plan: Model Improvement Plan. Version II Page 52 in C. P. a. R. Authority. The Water Institute of the Gulf, Baton Rouge, Louisiana.

Cowan, J.H.J., Deegan, L.A., Day, J.W., 2014. Fisheries in a changing delta. In: Day, J.W., Kemp, G.P., Freeman, A.M., Muth, D.P. (Eds.), Perspectives on the Restoration of the Mississippi Delta: the once and Future Delta. Springer Netherlands, Dordrecht, pp. 99–109.

Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32, 476–496.

Day, J.W., Shaffer, G.P., Britsch, L.D., Reed, D.J., Hawes, S.R., Cahoon, D., 2000. Pattern and process of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. Estuaries 23, 425–438.

Day, J.W.J., Boesch, D.F., Clairain, E.J., Kemp, G.P., Laska, S.B., Mitsch, W.J., Orth, W., Mashriqui, H., Reed, D.J., Shabman, L., Simenstad, C.A., Streever, B.J., Twilley, R.R., Watson, C.C., Wells, J.T., Whigham, D., 2007. Restoration of the Mississippi delta: lessons from hurricanes Katrina and Rita. Science 315, 1679–1684.

Ernst, C.H., Lovich, J.E., 2009. Turtles of the United States and Canada, second ed. Johns Hopkins Press, Baltimore, Maryland.

Feinberg, J.A., Burke, R.L., 2003. Nesting ecology and predation of diamondback terrapins, *Malaclemys terrapin*, at Gateway national recreation area. N. Y. J. Herpetol. 37, 517–526.

Hay, W.P., 1917. Artificial propagation of the diamondback terrapin. Bull. U. S. Bur. Fish. 24, 1–20.

Kindt, R., Coe, R., 2005. Tree Diversity Analysis: a Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agroforestry Centre (ICRAF), Nairobi.

Lazell, J.D., Auger, P.J., 1981. Predation on diamondback terrapin (*Malaclemys terrapin*) eggs by dunegrass (*Ammophila breviligulata*). Copeia 723–724.

LOSCO, 2010. Louisiana Oil Spill Coordinator's Office. www.losco.state.la.us.

NOAA Office for Coastal Management, 2016. In: N. O. A. A. Administration (Ed.), General Coastline and Shoreline Mileage of the United States, pp. 1–2. https://coast.noaa.gov/data/docs/states/shorelines.pdf.

Osland, M.J., Enwright, N.M., Day, R.H., Gabler, C.A., Stagg, C.L., Grace, J.B., 2016. Beyond just sea-level rise: considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. Global Change Biol. 22, 1–11.

Pearson, S.H., Wiebe, J., 2014. Evaluation of diamondback terrapin (*Malaclemys terrapin*) abundance, distribution and reproduction throughout coastal Louisiana 2014 research. In: Management and Wildlife Education Symposium, Baton Rouge, LA.

Roosenburg, W.M., 2008. In: Final Report for the IVth Symposium on the Ecology, Status, and Conservation of the Diamondback Terrapin, . www.dtwg.org.

Roosenburg, W.M., Dunham, A.E., 1997. Allocation of reproductive output: egg and clutch size variation in the diamondback terrapin. Copeia 2, 290–297.

Roosenburg, W.M., Place, A.R., 1994. Nest predation and hatchling sex ratio in the diamondback terrapin, Implications for management and conservation. In: Toward a Sustainable Coastal Watershed: the Chesapeake Experiment. Chesapeake Research Consortium, Norfolk VA, pp. 65–70.

Roosenburg, W.M., Spontak, D.M., Sullivan, S.P., Matthews, E.L., Heckman, M.L., Trimbath, R.J., Dunn, R.P., Dustman, E.A., Smith, L., Graham, L.J., 2014. Nesting habitat creation enhances recruitment in a predator free environment: *malaclemys* nesting at the Paul S. Sarbanes ecosystem restoration project. Restor. Ecol. 22, 815–823.

Seigel, R.A., 1980a. Nesting habits of diamondback terrapin (*Malaclemys terrapin*) on the Atlantic coast of Florida. Trans. Kans. Acad. Sci. 83, 239–246.

Seigel, R.A., 1980b. Courtship and mating behavior of the diamondback terrapin, *Malaclemys terrapin tequesta*. J. Herpetol. 14, 420–421.

Seigel, R.A., 1984. Parameter of two populations of the diamondback terrapin (*Malaclemys terrapin*) on the Atlantic coast of Florida. In: Seigel, R.A., Hunt, L.E., Knight, J.L., Malaret, L., Zushlag, N.L. (Eds.), Vertebrate Ecology and Systematics - a Tribute to Henry S. Fitch. University of Kansas, Lawrence, Kansas, pp. 7–87 Museum of Natural History.

Selman, W., Baccigalopi, B., Baccigalopi, C., 2014. Distribution and abundance of diamondback terrapins (*Malaclemys terrapin*) in southwestern Louisiana. Chelonian Conserv. Biol. 13, 131–139.

Sheridan, C.M., Spotila, J.R., Bien, W.F., Avery, H.W., 2010. Sex-biased dispersal and natal philopatry in the diamondback terrapin, Malaclemys terrapin. Mol. Ecol. 19, 5497–5510.

Silliman, B.R., Bertness, M.D., 2002. A trophic cascade regulates salt marsh primary production. Proc. Natl. Acad. Sci. 99, 10500–10505.

Tucker, A.D., Gibbons, J.W., Greene, J.L., 2001. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. Can. J. Zool. 79, 2199–2209.

Wnek, J.P., Bien, W.F., Avery, H.W., 2013. Artificial nesting habitats as a conservation strategy for turtle populations experiencing global change. Integr. Zool. 8, 209–221.

Zimmerman, T.D., 1989. Latitudinal Reproduction Variation of the Salt Marsh Turtle, the Diamondback Terrapin (Malaclemys Terrapin). College of Charleston, Charleston, South Carolina.