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# Kemp's Ridley Sea Turtle (*Lepidochelys kempii*) Nesting on the Texas Coast: Geographic, Temporal, and Demographic Trends Through 2014

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**Kemp's ridley (*Lepidochelys kempii*) is the world's most endangered sea turtle species, and nests primarily on the Gulf of Mexico coast in Mexico. In 1978, a binational project was initiated to form a secondary nesting colony of this species in south Texas at Padre Island National Seashore (PAIS), as a safeguard against extinction. During 1978–2014, we documented 1,667 Kemp's ridley nests in Texas, with 56% found at PAIS. Most nests (89%) found in south Texas were from wild-stock turtles; south Texas is the northern extent of the documented historic nesting range for the species. We documented nesting in north Texas starting in 2002, and most nests (53%) found there were from turtles that had been head-started (reared in captivity for 9–11 mo), and released off the Texas coast as yearlings. Kemp's ridley nesting increased in Texas during the mid-1990s through 2009, before annual nest numbers dropped in 2010, rebounded and plateaued in 2011 and 2012, and then decreased again in 2013 and 2014. Annual numbers of nests found in Texas and Mexico followed similar trends and were correlated ( $R^2 = 0.95$ ). We examined nesting turtles for presence of tags at 55% of the nests located in Texas. Of the Kemp's ridleys we examined during 2000–14, the annual percentage of apparent neophytes decreased and the annual percentage of remigrants increased over time. Mean annual remigration intervals of Kemp's ridleys increased steadily from 1.9 yr in 2008 to 3.3 yr in 2014. These changes in demographic parameters are critical to understanding the recent fluctuation in the number of nesting Kemp's ridleys and will be used in population models to investigate possible causes of the recent and sudden decline of nesting Kemp's ridleys in Texas and Mexico.**

## INTRODUCTION

The Kemp's ridley (*Lepidochelys kempii*) is the world's most endangered sea turtle species. Most Kemp's ridleys nest on the Gulf Coast of Mexico, with the epicenter of nesting near Rancho Nuevo, Tamaulipas, Mexico. Kemp's ridley nesting declined precipitously between the 1940s and the mid-1980s (Márquez et al., 2005). In the 1970s, the National Park Service established the binational Kemp's ridley recovery project. This project's aims included protection of nesting turtles and nests at the primary nesting beach of Rancho Nuevo and formation of a secondary nesting colony at Padre Island National Seashore (PAIS), Texas, United States, where this species is a native nester (Shaver and Caillouet, 1998, 2015; Shaver, 2005; Caillouet et al., 2015). The secondary nesting colony at Padre Island provides a safeguard for the species against a political or environmental catastrophe at the primary nesting beach.

The PAIS Restoration Program was designed around the imprinting hypothesis, whereby sea turtles are thought to return to nest in the region

where they were hatched through imprinting or another natal homing mechanism (Bowen et al., 1992, 1998; Bowen and Karl, 2007). From 1978–88, a cumulative total of 22,507 Kemp's ridley eggs were collected at the primary nesting beach in Rancho Nuevo for experimental imprinting to PAIS. The eggs were incubated in PAIS sand and hatched at PAIS, and the resulting hatchlings were allowed to crawl down the beach and enter the surf at PAIS in the hope that they would imprint on this region and return there to nest at adulthood. From these, 15,875 hatchlings were captured in the surf and transported to the National Marine Fisheries Service (NMFS) laboratory in Galveston, Texas for 9–11 mo of captive rearing termed head-starting (Fontaine and Shaver, 2005; Shaver, 2005; Shaver and Wibbels, 2007). The head-start program ensured these hatchlings would survive the vulnerable hatchling life-stage before release into the wild. It was hoped that these “Padre Island-imprinted head-starts” would return to PAIS to nest, to form a secondary nesting colony there.

Additionally, from 1978–2000, more than 10,000 hatchlings that emerged from nests

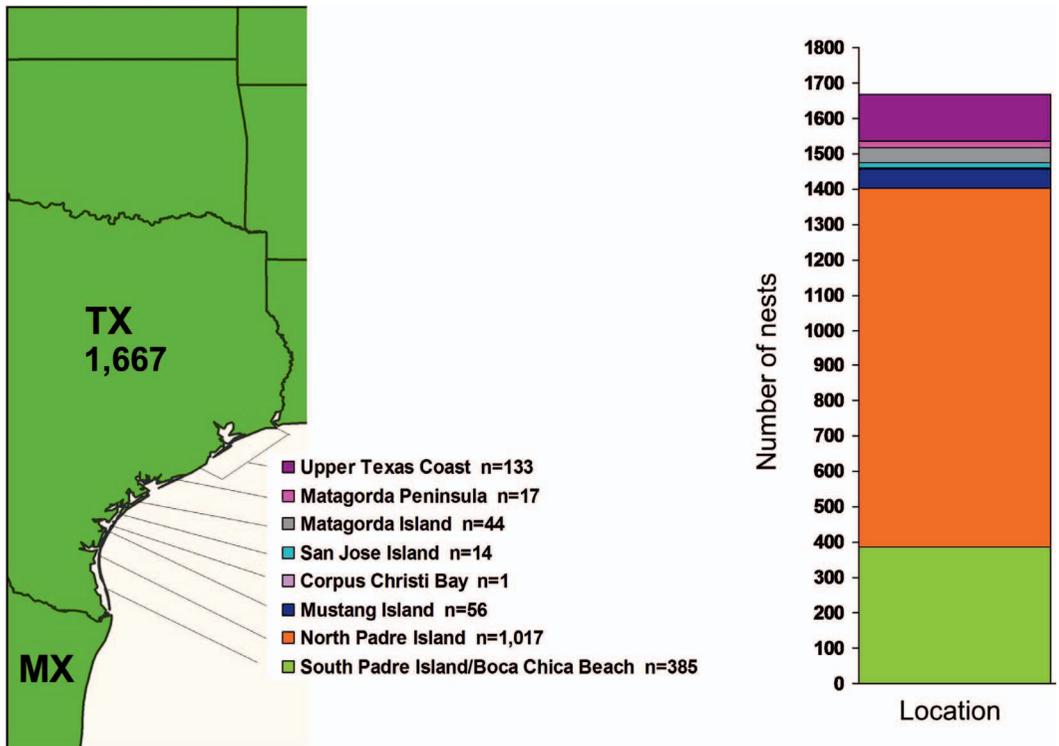


Fig. 1. Locations of Kemp's ridley turtle (*Lepidochelys kempii*) nests found along the Texas coast from 1978–2014. The south Texas coast includes Mustang Island southward to the U.S./Mexico border. The north Texas coast includes the Texas/Louisiana border to San Jose Island.

incubated in a corral at Rancho Nuevo were allowed to crawl down the beach and enter the surf at Rancho Nuevo, but were captured in the surf and then transported to the NMFS laboratory for head-starting (Shaver, 2005; Shaver and Wibbels, 2007). The objective of this hatchling translocation was for these “Mexico-imprinted head-starts” to return to Mexico to nest, to help compensate the Mexican nesting population for the translocation of eggs to Texas.

The documented historic nesting range for Kemp's ridley (i.e., before egg and hatchling translocations) is from south Texas (Mustang Island to the U.S./Mexico border; Fig. 1) through Veracruz, Mexico. Nest detection and protection efforts began in Mexico at Rancho Nuevo during 1966, and expanded to other beaches in Tamaulipas and Veracruz as larger numbers of nests were recorded there (NMFS et al., 2011). From 1966 until recent years, nearly all Kemp's ridley clutches found in Mexico were protected in beach hatcheries called corrals. In recent years, too many nests have been located in Rancho Nuevo to logistically transfer all to corrals, so a portion have been left to incubate

unprotected on the beach (*in situ*) (Bevan et al., 2014). Patrols to monitor for nesting Kemp's ridleys and protect nests began in Texas at PAIS during 1986 and expanded as nests were detected elsewhere in the state (NMFS et al., 2011). Nearly all clutches found in Texas were protected in an incubation facility or corrals (Shaver and Caillouet, 2015).

After decades of binational conservation efforts, Kemp's ridley nesting increased exponentially from the mid-1990s through 2009. The Kemp's Ridley Sea Turtle Recovery Team and population modelers expected that with continued high egg survival these increases would continue for several years, and were cautiously optimistic that the Kemp's ridley population was on the road to recovery (Heppell et al., 2005, 2007; NMFS et al., 2011). However, exponential increases in nesting ended in 2010 (the year of the Deepwater Horizon [DWH] Oil Spill) and parallel declines in the number of Kemp's ridleys nesting in Texas and Mexico have renewed concern about the status of this species (Caillouet, 2014; Plotkin and Bernardo, 2014; Shaver and Caillouet, 2015).

Here we examine spatial, temporal, and demographic trends of Kemp's ridley nesting in Texas, and the contribution of translocation and head-starting efforts to that nesting, collected by long-term beach patrol monitoring, tagging of nesting turtles, and nest protection. We compare recent nesting trends in Texas and Mexico, and discuss whether demographic parameter data collected in Texas may have broader applicability for the species. Quantification of demographic parameters is necessary for assessing population status (Heppell et al., 2007; Witherington et al., 2009; Bolton et al., 2011; Lamont et al., 2012) and analyzed trends in these parameters may be important to understanding possible causes for recent changes in the nesting trajectory for this species.

#### METHODS

Kemp's ridleys nest mostly during daylight hours, and we located nests in Texas during diurnal patrols or opportunistically through reports from the public or others working on the beach. Patrol coverage varied temporally and spatially as nesting increased and expanded in Texas. The largest and most consistent patrol effort was in south Texas, where nesting occurred historically and most nesting currently occurs. We began systematic patrols to detect and protect nesting Kemp's ridley turtles and their eggs in Texas on North Padre Island (including PAIS) in 1986, where they were conducted only a few days a week during the first decade, but increased to 7 d a week from 1995–97 (Shaver, 2005). From 1998 onward, we traversed the North Padre Island beachfront repeatedly each day. This coverage increased the likelihood of observing nesting Kemp's ridleys and locating their nests. We began repeated daily patrols elsewhere in Texas starting on Boca Chica Beach in 1999 and South Padre Island in 2000. By 2005, we conducted patrols on the entire Texas Gulf of Mexico beachfront (approximately 590 km) to some extent during the nesting season, although patrols were not conducted daily in some locations in north Texas (upper Texas coast to San Jose Island) (Fig. 1) (NMFS et al., 2011). We recorded the cumulative distance patrolled and tallied this annually. We conducted extensive public education and training statewide to encourage nest reporting by the public and others working on the beach.

Whenever possible, we examined nesting Kemp's ridleys for the presence of living, passive

integrated transponder (PIT), coded wire, or metal tags that could link them to head-starting or to a previous nesting event (see Shaver and Caillouet, 2015). We applied PIT and metal tags to those nesters that lacked them. We measured most nesting turtles examined for straight carapace length (SCL) and curved carapace length (CCL) from the center of the nuchal notch to the tip of the longest postcentral scute. When only CCL was measured, we converted CCL to SCL using the conversion equation derived for stranded Kemp's ridley turtles by Teas (1993).

We attempted to locate and confirm nests at all locations where nesting Kemp's ridley turtles or their tracks were found in Texas (see Shaver and Caillouet, 2015). We recorded geographic location and lay date (when known) for all confirmed nests. We moved eggs from all nests located during egg laying from 1979–2014 to an incubation facility or corral to enhance recruitment (Shaver and Caillouet, 2015). A few nests were not found at egg laying and were incubated unprotected (*in situ*). After hatching of all protected nests, we enumerated clutch size, hatching success (number of live and dead hatchlings/clutch size), emergence success (number of live hatchlings/clutch size), and number of hatchlings released. However, these parameters could not be accurately quantified for *in situ* nests due to predation, other disturbances at the nest site, or lack of monitoring through hatchling release.

We tallied nests by geographic area, nest date and year, and origin of nester (unexamined, wild stock, Padre Island-imprinted head-start, Mexico-imprinted head-start, or unclear wild or head-start [see Shaver and Caillouet, 2015]). We plotted the annual number of nests found in Texas and Mexico from 1978–2014, and used correlation to examine the relationship between the numbers of nests found annually in two areas.

We conducted more detailed analyses with data from 2000–14, when nest detection patrols were more robust and larger numbers of nesting turtles and nests were found. We standardized the annual number of nests by patrol effort and fit curves to the data, to outline an overall nesting trend while controlling for annual variations in patrol effort. We quantified parameters of nesting season, nester SCL, the percentage of nests at which nesting turtles were examined, the percentage of turtles classified as apparent neophytes (turtle documented nesting

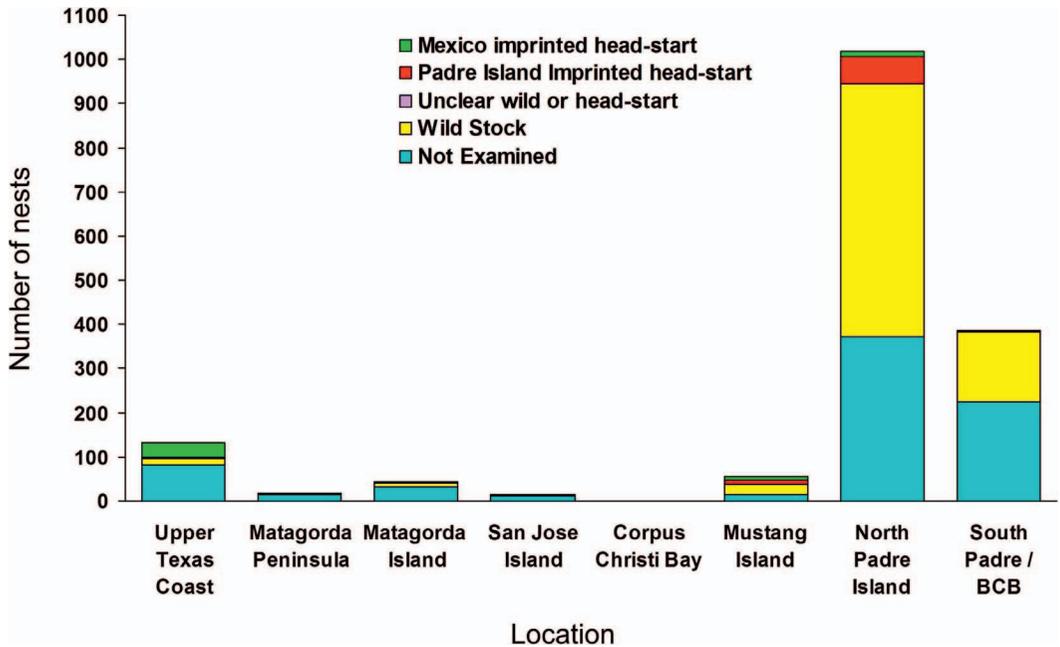


Fig. 2. Locations for wild and head-started Kemp's ridley turtle (*Lepidochelys kempii*) nests along the Texas coast from 1978–2014. Colors denote the identified sources of the nesting females.

for the first time at any beach in the United States or Mexico) or remigrants (turtle previously documented nesting at any beach in the United States or Mexico), clutch frequency (number of nests per female examined per nesting season), remigration interval, clutch size, and emergence success. We fitted linear regressions to identify any linear trends in these parameters through time. We repeated these analyses for three quantifiers of the nesting season (Julian date first nest found, Julian date last nest found, duration [number of days between when the first and last nests were found]) for years 2004–14, when larger numbers of nests were found, to reduce the bias of small sample sizes in quantifying these parameters for years 2000–03 when few nests ( $n = 8\text{--}38$ ) were located. We also repeated this analysis for remigration interval for years 2008–14, when larger numbers of remigrants were found, to reduce the bias of small sample sizes in quantifying this parameter during years 2000–07 when few remigrants ( $n = 0\text{--}9$ ) were located. We also used linear regression to analyze the relationship between the onset and duration of the nesting season, for years 2000–14, and 2004–14. Significant linear or curvilinear relationships are plotted for analyses involving at least years 2000–14. We calculated overall mean SCL, clutch

frequency, remigration interval, clutch size, and emergence success for years 2000–14 combined. Mean annual SCL, clutch frequency, clutch size, and emergence success were compared for years 2000–14 using analysis of variance. When normality tests failed, equivalent nonparametric tests were used. Alpha was set at 0.05 for all tests.

## RESULTS

From 1978–2014, 1,667 Kemp's ridley nests were documented in Texas, including 1,606 nests that were protected and 61 that incubated *in situ*. Of the 1,667 nests, 87.5% were found in south Texas, extending from Mustang Island to the U.S./Mexico border, and 12.5% in north Texas, extending from the upper Texas coast to San Jose Island (Fig. 1).

Nesting turtles were examined for tags at 916 of the 1,667 Texas nests (Fig. 2). Of these, 784 nests were from wild-stock turtles, 69 from Padre Island-imprinted head-start turtles, 57 from Mexico-imprinted head-start turtles, and six from turtles that we were uncertain were wild or head-start. For nests at which the nesting turtles were examined in south Texas, most (89.4%) were from wild-stock turtles, although 7.9% were from Padre Island-imprinted head-start turtles and 2.7% were from Mexico-imprinted head-start

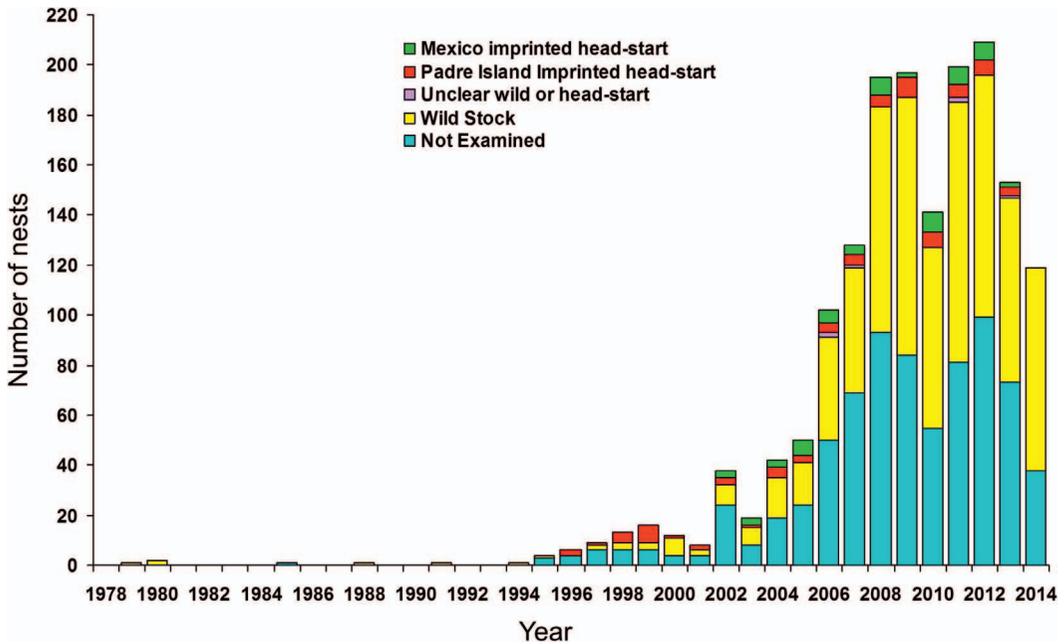


Fig. 3. Annual nest counts of Kemp's ridley turtles (*Lepidochelys kempii*) found on the Texas coast from 1978–2014. Colors denote the identified sources of the nesting females.

turtles (Fig. 2). In contrast, in north Texas, most (51.7%) nests were from Mexico-imprinted head-start turtles, although 1.5% were from Padre Island-imprinted head-start turtles, 9.1% were from turtles that we were uncertain were wild or head-start, and 37.9% were from wild-stock turtles (Fig. 2). Mexico-imprinted head-start turtles were first found nesting in Texas in 2002 (Fig. 3), the same year that Kemp's ridley nests were first confirmed in north Texas.

Overall, the annual Texas Kemp's ridley nest numbers increased from 1995–2009 (year =  $1998.822 + (0.0568 \times \text{number of nests})$ ,  $R^2 = 0.732$ ,  $P < 0.001$ ). Record numbers of nests were recorded during six consecutive years from 2004–09 and during 2011 and 2012 (Figs. 3, 4). However, the 2011 ( $n = 199$ ) and 2012 ( $n = 209$ ) numbers of nests were only slight increases from the 197 nests found during 2009, and many fewer nests were recorded during 2010 ( $n = 141$ ), 2013 ( $n = 153$ ), and 2014 ( $n = 119$ ). The annual number of Kemp's ridley nests found in Mexico and Texas from 1978–2014 trended similarly (Fig. 4) and were highly correlated,  $R^2 = 0.949$ ,  $P < 0.001$  (Table 1). Patrol efforts in Texas generally increased from 1986–2014 (Fig. 5). The best fit to the annual nest totals from 2000–14 standardized for patrol effort was a third-order polynomial curve,  $R^2 = 0.9029$  (Fig. 6).

For 1978–2014, Kemp's ridley nests were found in Texas from April through mid-July, with a peak from 16 April through 15 June (Fig. 7). Between 2000 and 2014, when 8–209 nests were recorded annually, the seasonal phenology of nesting by date varied slightly each year (Fig. 8). However, the Julian dates of first ( $R^2 = 0.000$ ,  $P = 0.993$ ) and last ( $R^2 = 0.211$ ,  $P = 0.085$ ) nests and the cumulative 20% ( $R^2 = 0.000$ ,  $P = 0.969$ ), 50% ( $R^2 = 0.158$ ,  $P = 0.142$ ), and 80% ( $R^2 = 0.002$ ,  $P = 0.875$ ) percentiles of annual nest totals did not significantly increase or decrease through time (Table 1; Fig. 9). From 2000–14, the nesting season duration ranged from 51–86 d ( $\bar{x} = 72.9$  d,  $SE = 2.9$  d,  $n = 15$ ) and increased slightly, but not significantly through time ( $R^2 = 0.177$ ,  $P = 0.119$ ) (Table 1; Fig. 10). However, for years 2004–14 (when more than 40 nests were found each year), the Julian dates of the last nest ( $R^2 = 0.549$ ,  $P = 0.009$ ) and the nesting season duration ( $R^2 = 0.379$ ,  $P = 0.044$ ) increased significantly through time (Table 1). For 2000–14, the nesting season duration was unrelated to the onset of the nesting season ( $R^2 = 0.183$ ,  $P = 0.112$ ), but for years 2004–14 the nesting season lasted longer when nesting began earlier ( $R^2 = 0.478$ ,  $P = 0.019$ ) (Table 1; Fig. 11).

For 2000–14 when 4–82 individuals were measured, the mean SCL for all turtles was 63.1 cm, ( $SE = 0.1$  cm, range = 54.8–72.6 cm,  $n =$

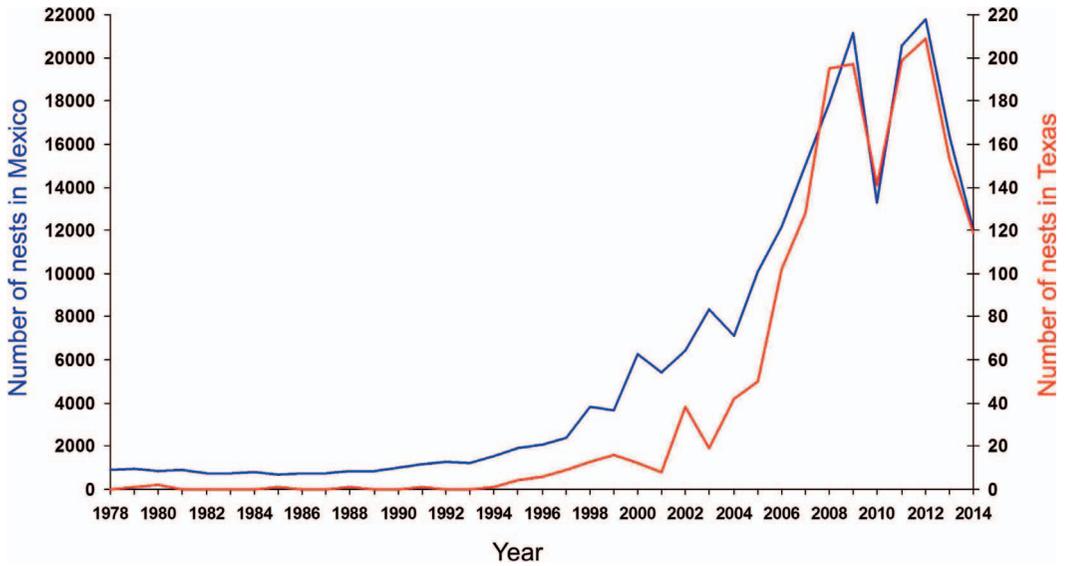


Fig. 4. Annual nest counts of Kemp’s ridley turtles (*Lepidochelys kempii*) in Texas and Mexico from 1978–2014. Data from Mexico courtesy of Gladys Porter Zoo and Comisión Nacional de Áreas Naturales Protegidas (CONANP).

642). The annual mean SCL ranged from 62.1–63.5 cm ( $\bar{x}$  = 62.9 cm, SE = 0.1 cm, n = 15). Annual mean SCL increased slightly, but significantly ( $R^2$  = 0.296,  $P$  = 0.036), maximum SCL

increased significantly ( $R^2$  = 0.669,  $P$  < 0.001), and minimum SCL decreased significantly through time ( $R^2$  = 0.390,  $P$  = 0.013) (Table 1; Fig. 12). However, annual median SCLs did not

TABLE 1. Results of correlation and linear regression analyses for numbers of nests found in Mexico and Texas (for years 1978–2014), and for relationships in Figs. 8–14 (for years 2000–2014; see exceptions in footnotes).

Linear regression equations	$P$	$R^2$
No. of nests in Mexico = 1787.061 + (94.693 × no. of nests in Texas)	< 0.001**	0.949
Nesting season duration (days) = -2063.155 + (1.064 × year)	0.119	0.177
Nesting season duration (days) = -3853.500 + (1.955 × year) <sup>a</sup>	0.044**	0.379
Julian date last nest found = -1961.989 + (1.068 × year)	0.085	0.211
Julian date last nest found = -3251.655 + (1.709 × year) <sup>a</sup>	0.009**	0.549
Julian date 80% of nests found = -2.493 + (0.0786 × year)	0.875	0.002
Julian date 50% of nests found = -1157.582 + (0.646 × year)	0.142	0.158
Julian date 20% of nests found = -159.773 - (0.0179 × year)	0.969	0.000
Julian date first nest found = 101.165 + (0.00357 × year)	0.993	0.000
Julian date first nest found = 601.845 - (0.245 × year) <sup>a</sup>	0.713	0.015
Julian date first nest found = 126.546 - (0.250 × nesting season duration)	0.112	0.183
Julian date first nest found = 139.876 - (0.426 × nesting season duration) <sup>a</sup>	0.019**	0.478
Maximum SCL <sup>b</sup> (cm) = -751.903 + (0.409 × year)	< 0.001**	0.669
Mean SCL (cm) = -41.203 + (0.0519 × year)	0.036**	0.296
Minimum SCL (cm) = 585.794 - (0.263 × year)	0.013**	0.390
% of nests at which nesting turtles examined = -340.066 + (0.197 × year)	0.611	0.020
% of nesting turtles examined that were neophytes = 4112.905 - (2.015 × year)	0.034**	0.302
% of nesting turtles examined that were remigrants = -4012.905 + (2.015 × year)	0.034**	0.302
Mean clutch frequency (nests) = -50.444 + (0.0258 × year)	< 0.001**	0.738
Mean remigration interval (years) = -416.16 + (0.2083 × year) <sup>c</sup>	< 0.001**	0.916
Mean clutch size (eggs) = 238.069 - (0.0704 × year)	0.720	0.010
Mean emergence success (%) = -1586.224 + (0.831 × year)	0.031**	0.312

<sup>a</sup> Years 2004–14.

<sup>b</sup> SCL = straight carapace length.

<sup>c</sup> Years 2008–14.

\*\*  $P$  < 0.05.

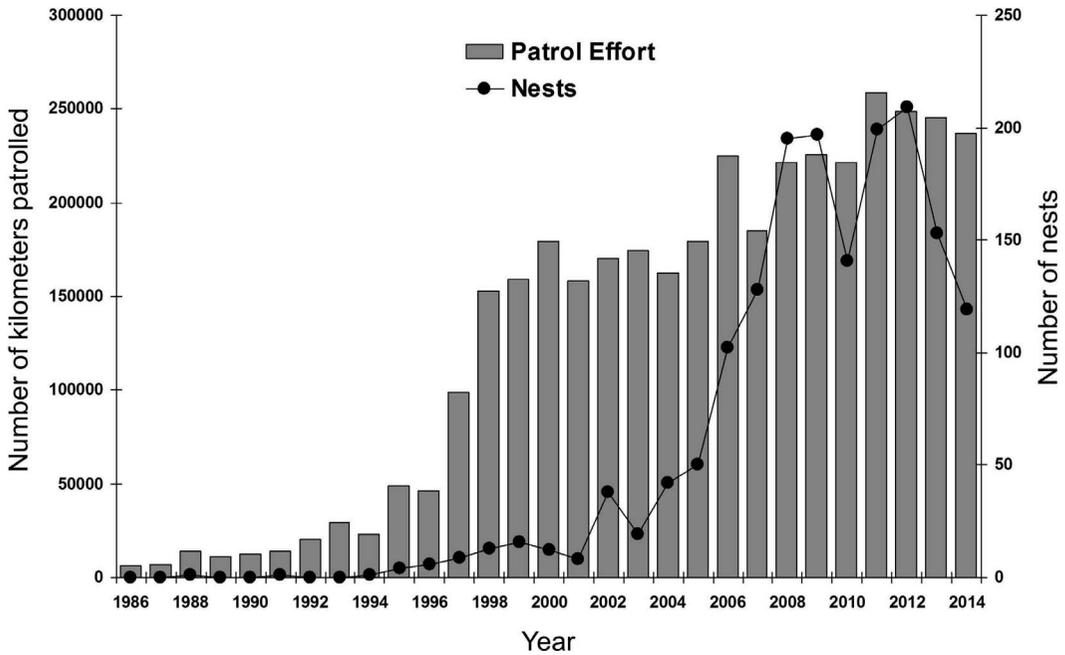


Fig. 5. Annual patrol effort (number of kilometers patrolled) and number of Kemp's ridley turtle (*Lepidochelys kempii*) nests found on the Texas coast from 1986–2014.

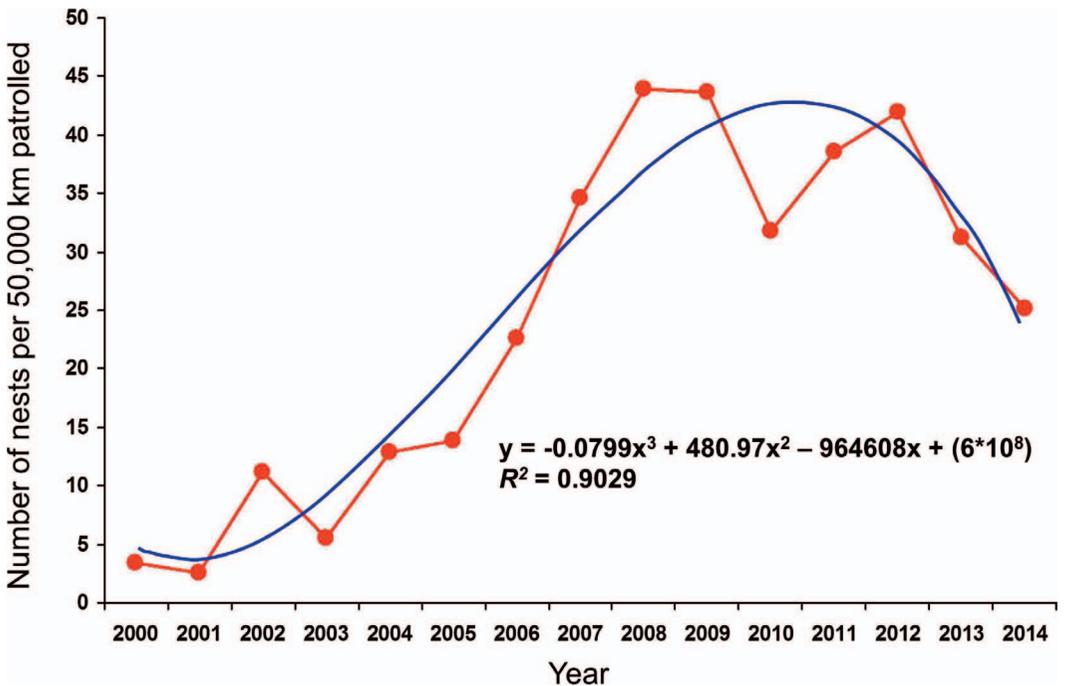


Fig. 6. Annual number of Kemp's ridley turtle (*Lepidochelys kempii*) nests found on the Texas coast from 2000–14 standardized for patrol effort, and third-order polynomial fitted to the data.

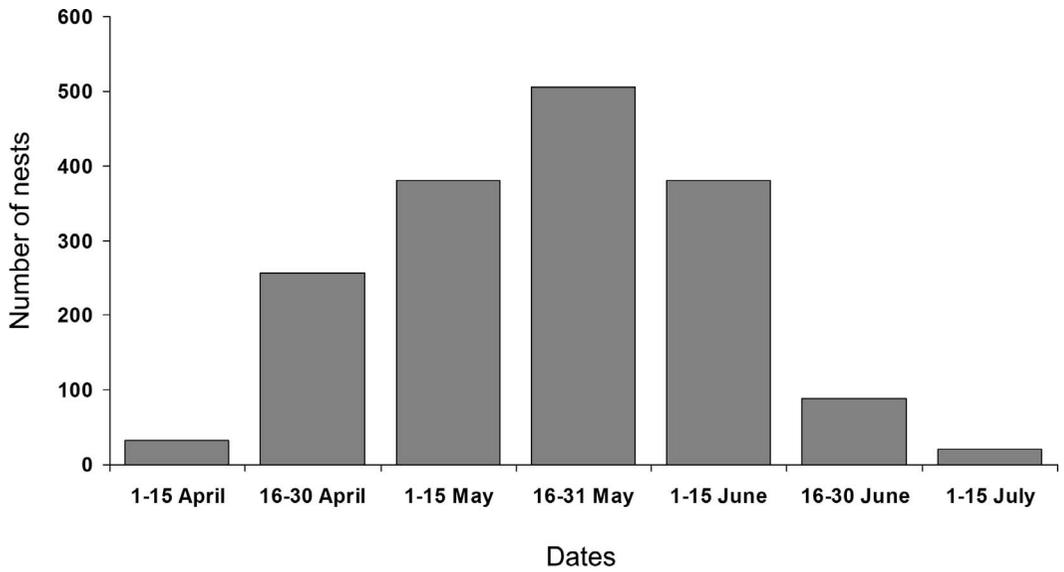


Fig. 7. Dates when Kemp’s ridley turtle (*Lepidochelys kempii*) nests were found on the Texas coast from 1978–2014.

differ significantly (Kruskal–Wallis  $H = 14.039$ ,  $df = 14$ ,  $P = 0.447$ ).

For 2000–14 when nesting turtles were examined for tags at 4–118 nests annually, the

percentage of nests at which nesting turtles were examined ranged from 46.1–68.1% ( $\bar{x} = 55.6\%$ ,  $SE = 1.6\%$ ,  $n = 15$ ) and remained relatively stable through time ( $R^2 = 0.020$ ,  $P = 0.611$ ) (Table 1;

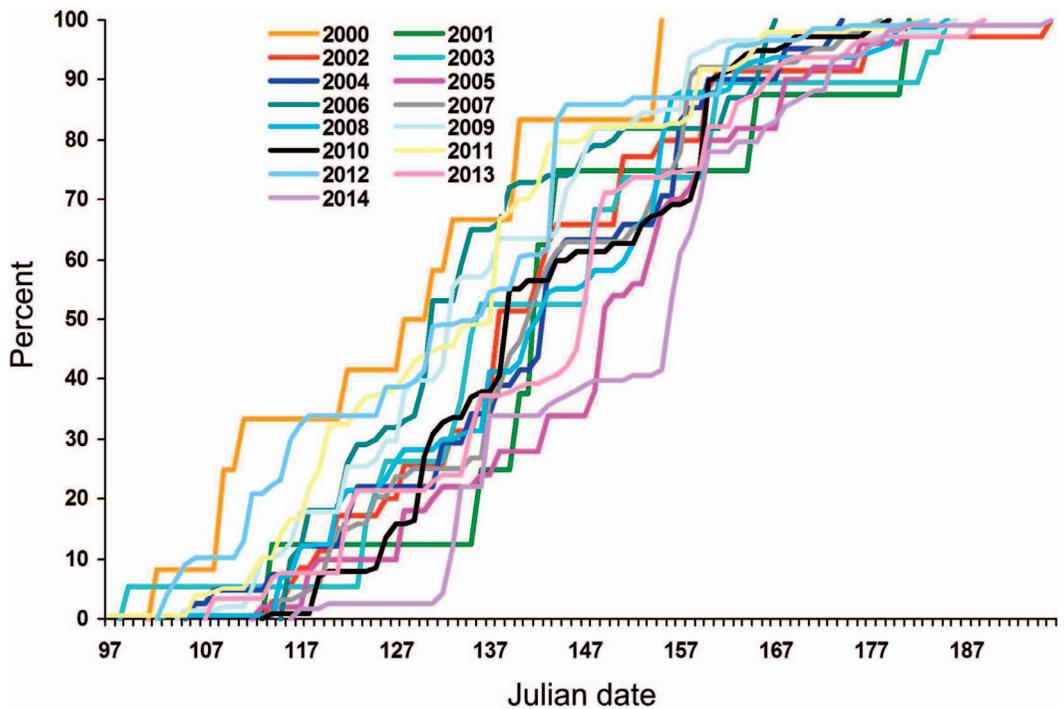


Fig. 8. Cumulative percentage of Kemp’s ridley turtle (*Lepidochelys kempii*) nests in Texas by Julian date, each year from 2000–14.

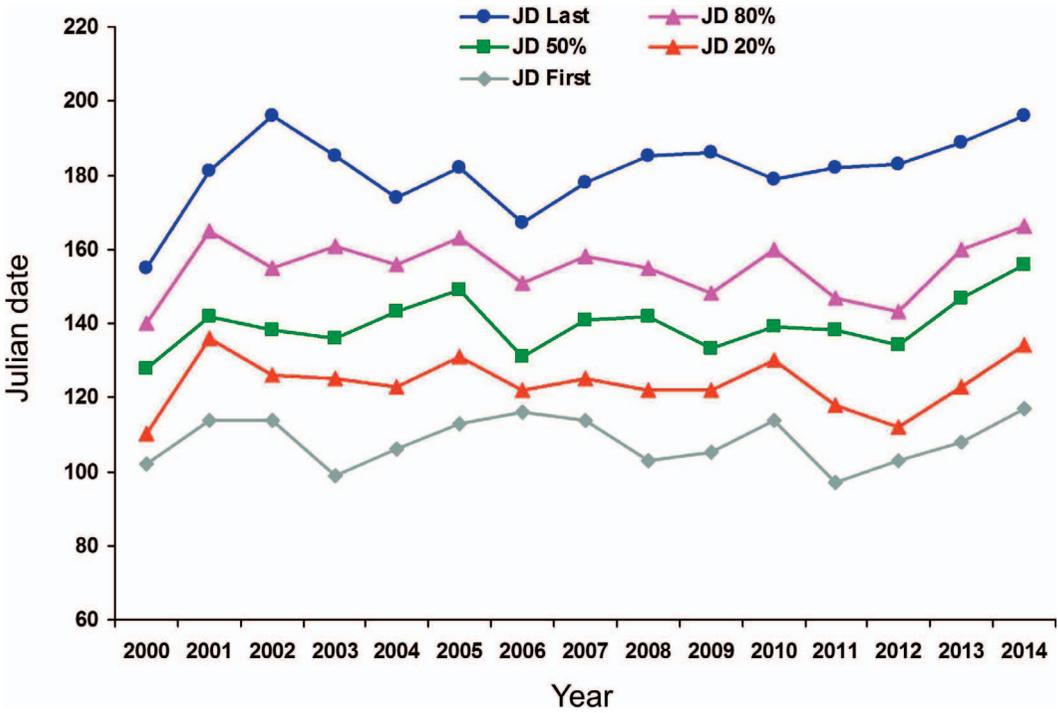


Fig. 9. Julian dates (JD) of first and last Kemp's ridley turtle (*Lepidochelys kempii*) nests, and 20, 50, and 80% of the cumulative percentiles of the annual nest totals in Texas for 2000-14.

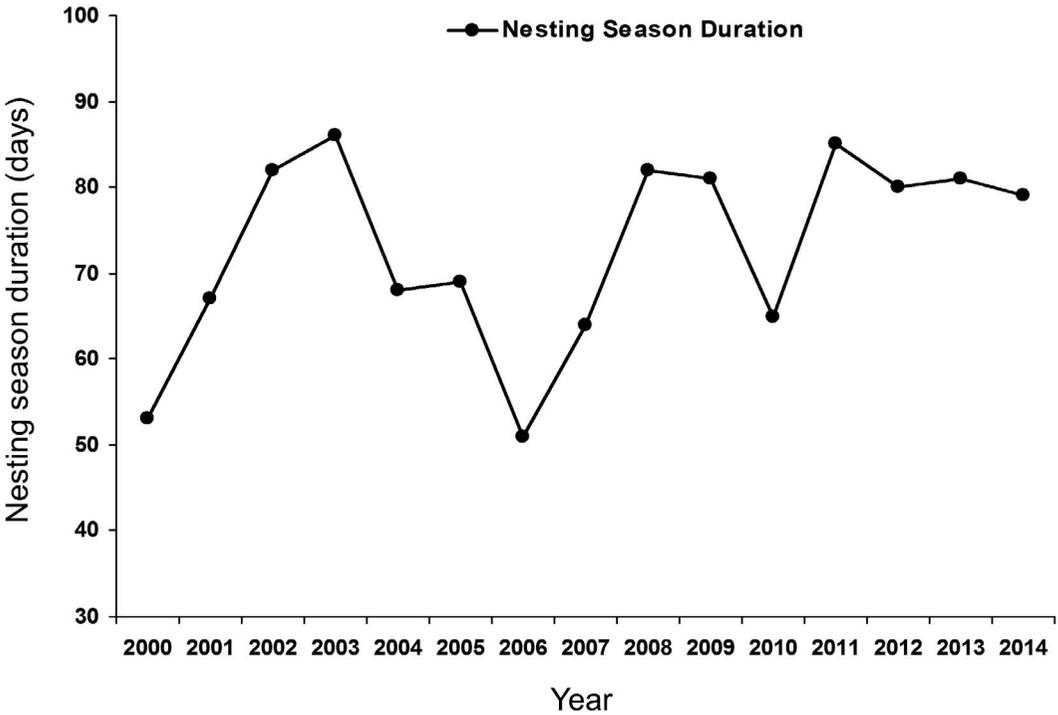


Fig. 10. Kemp's ridley turtle (*Lepidochelys kempii*) nesting season duration (days between discovery of the first and last nests of the year) in Texas for 2000-14.

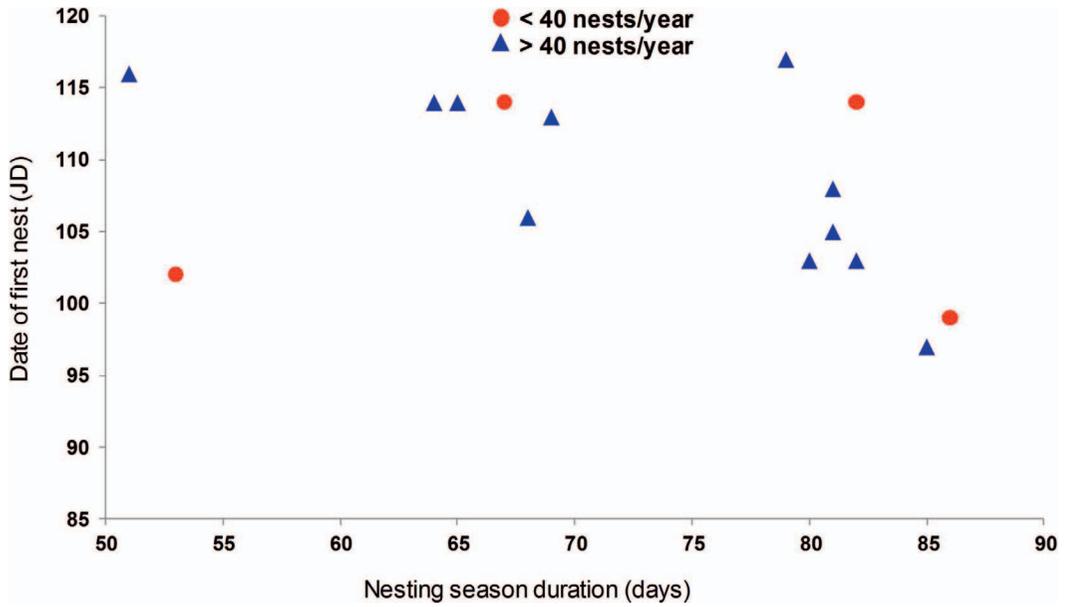


Fig. 11. Scatterplot of duration of the nesting season (number of days between when first and last nests found) and Julian date of the first nest of the Kemp’s ridley turtle (*Lepidochelys kempii*) nesting season in Texas from 2000–14. Different symbols are used to represent years when fewer and more than 40 nests were located.

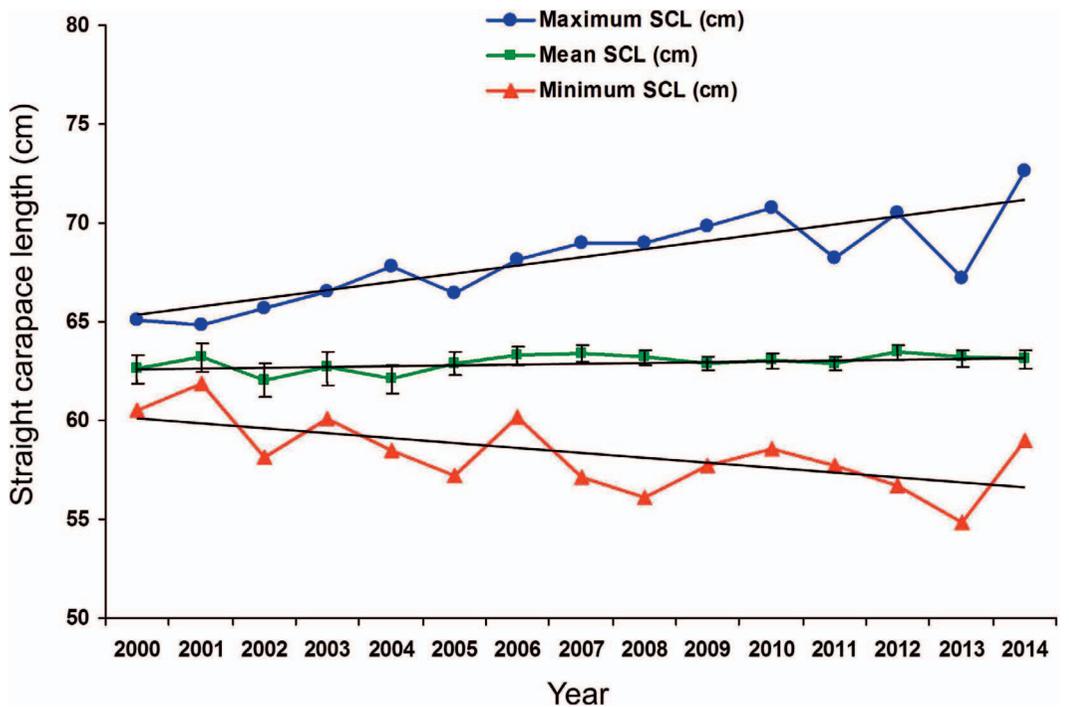


Fig. 12. Annual maximum, mean, and minimum straight carapace lengths (cm) of Kemp’s ridley turtles (*Lepidochelys kempii*) measured in Texas from 2000–14.

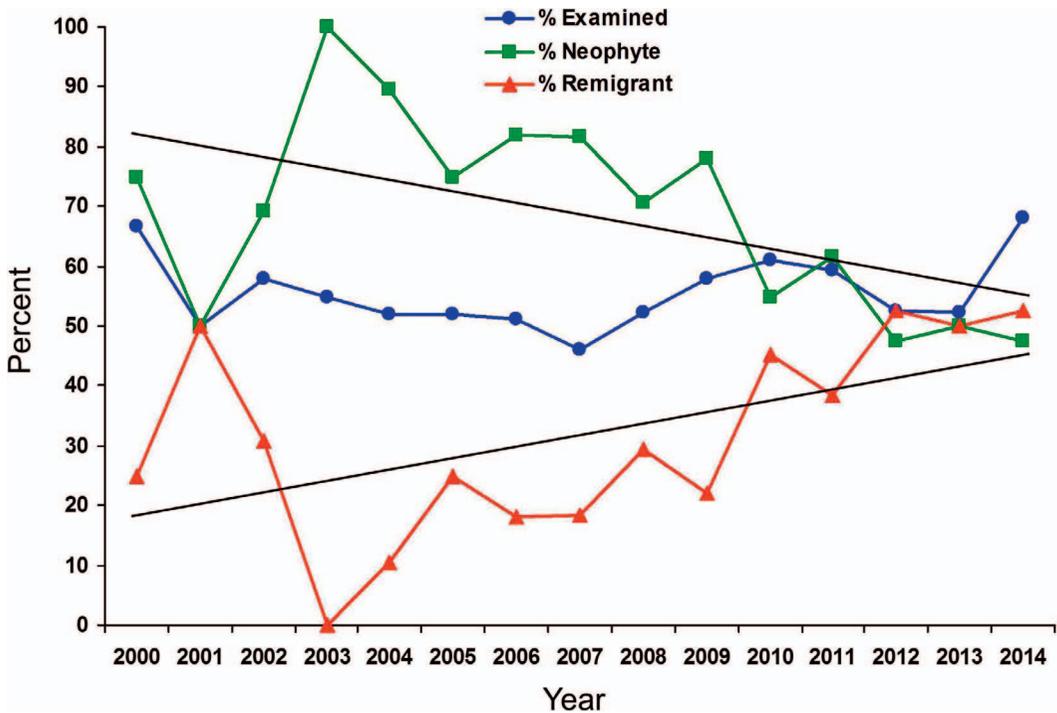


Fig. 13. Annual percentage of Kemp's ridley turtle (*Lepidochelys kempii*) nests at which nesting turtles were examined, and the percentage of individuals classified as neophytes or remigrants in Texas from 2000–14.

Fig. 13). During these years, 4–86 individuals were documented nesting each year. The annual percentage of turtles classified as apparent neophytes ranged from 47.4–100% and significantly decreased through time ( $R^2 = 0.302$ ,  $P = 0.034$ ) (Table 1; Fig. 13) while those turtles classified as remigrants ranged from 0–52.6% and significantly increased through time ( $R^2 = 0.302$ ,  $P = 0.034$ ).

The mean clutch frequency during years 2000–14 combined was 1.3 nests (SE = 0.02 nests, range = 1–3 nests,  $n = 675$ ). The annual mean clutch frequency ranged from 1.0–1.4 nests ( $\bar{x} = 1.2$  nests, SE = 0.03 nests,  $n = 15$ ) and increased slightly, but significantly, through time ( $R^2 = 0.738$ ,  $P < 0.001$ ) (Table 1; Fig. 14). However, annual median clutch frequency did not differ significantly between years (Kruskal–Wallis  $H = 20.384$ ,  $df = 14$ ,  $P = 0.118$ ).

The mean remigration interval for years 2000–14 combined was 2.7 yr, (SE = 0.1 yr, range 1–8 yr,  $n = 236$ ). Annual mean remigration interval (excluding 2003 with no remigrants recorded) ranged from 1.9–3.3 yr ( $\bar{x} = 2.6$  yr, SE = 0.1 yr,  $n = 14$ ). Sample sizes for the period 2000–07 ranged from 2–9 remigrants whereas sample sizes for 2008–14 ranged from 22–40 remigrants. Based

on the latter period having larger sample sizes, mean annual remigration intervals increased from a low of 1.9 yr in 2008 to a high of 3.3 yr in 2014 ( $R^2 = 0.916$ ,  $P < 0.001$ ) (Table 1; Fig. 14). The largest incremental increases occurred between 2010 and 2011 (from 2.5 to 2.9 yr) and between 2013 and 2014 (from 2.9 to 3.3 yr).

For 2000–14, when from 8–209 nests were recorded annually, the mean clutch size for all protected nests in all years combined was 96.7 eggs (SE = 0.4 eggs, range = 2–142 eggs,  $n = 1,551$ ). Annual mean clutch size ranged from 91–105 eggs ( $\bar{x} = 96.7$  eggs, SE = 0.8 eggs,  $n = 14$ ) and remained relatively stable through time ( $R^2 = 0.010$ ,  $P = 0.720$ ) (Table 1; Fig. 15). Annual median clutch size did not differ significantly (Kruskal–Wallis  $H = 20.108$ ,  $df = 14$ ,  $P = 0.127$ ).

The mean emergence success for all protected nests in years 2000–14 combined was 83.5% (SE = 0.5%, range = 0–100%,  $n = 1,551$ ). Annual mean emergence success ranged from 66.7–88.3% ( $\bar{x} = 81.2\%$ , SE = 1.7%,  $n = 15$ ) and increased significantly over time ( $R^2 = 0.312$ ,  $P = 0.031$ ) (Table 1; Fig. 15). Annual median emergence success differed significantly (Kruskal–Wallis  $H = 91.203$ ,  $df = 14$ ,  $P < 0.001$ ). The largest cohort of Kemp's ridley hatchlings

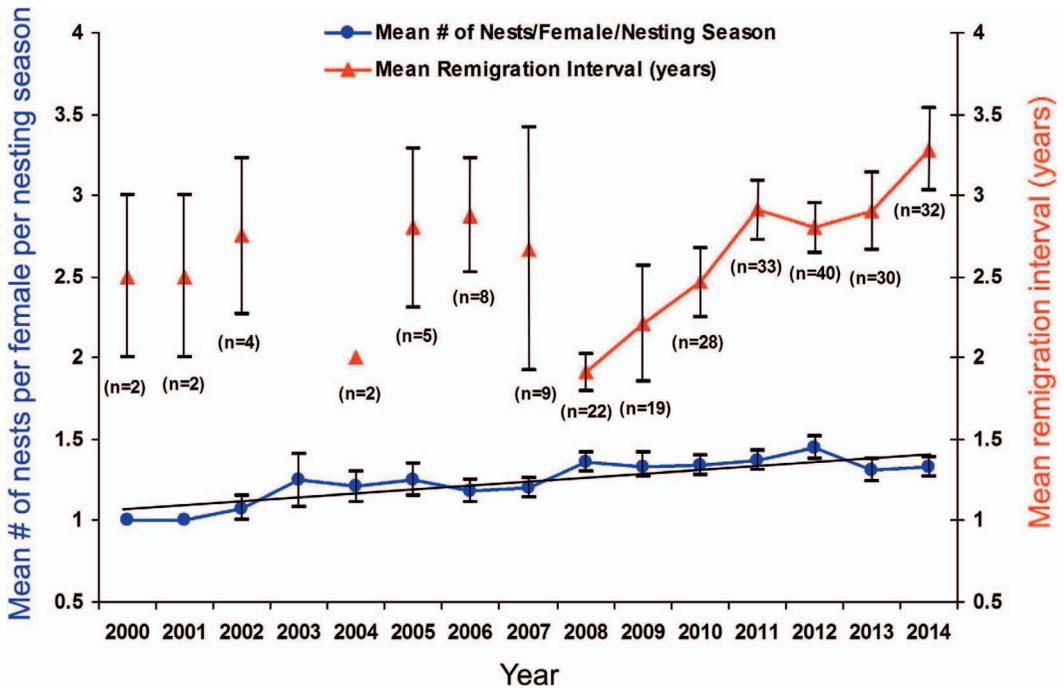


Fig. 14. Annual mean clutch frequency (nests per female per nesting season) and remigration interval (years) for Kemp’s ridley turtles (*Lepidochelys kempii*) documented nesting in Texas from 2000–14. Note that only one nest per female was documented during 2000 and 2001, few remigrants were observed between 2000 and 2007, and no remigrants were recorded nesting during 2003. n = the number of remigrants documented annually.

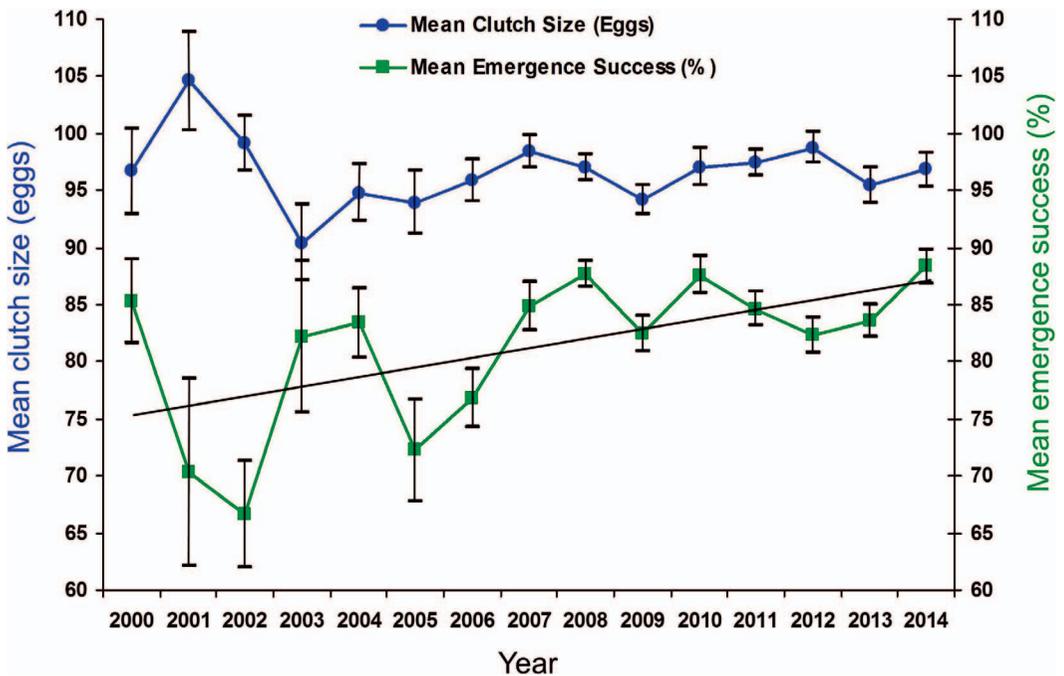


Fig. 15. Annual mean clutch size and emergence success for Kemp’s ridley turtle (*Lepidochelys kempii*) nests protected in Texas from 2000–14.

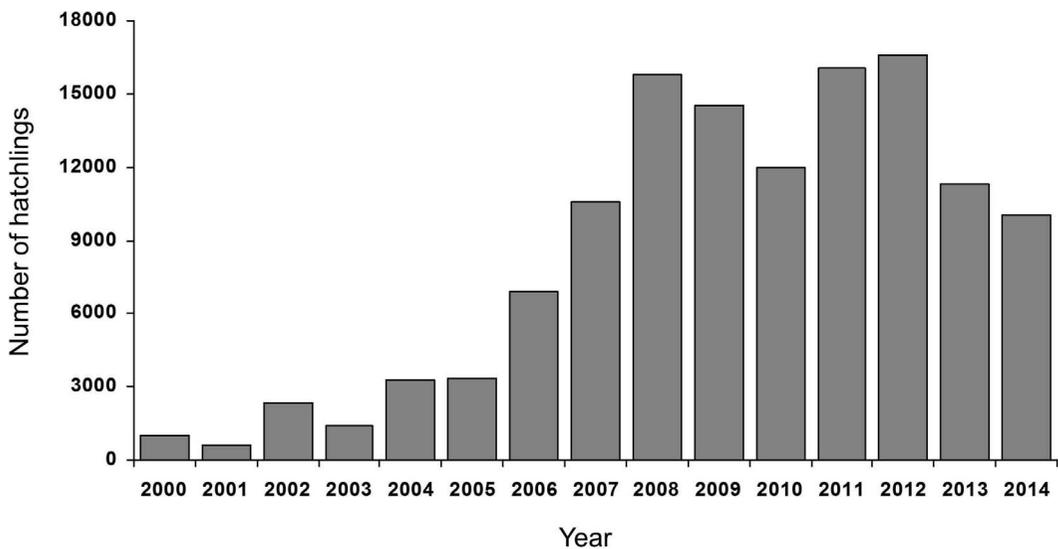


Fig. 16. Annual number of Kemp's ridley turtle (*Lepidochelys kempii*) hatchlings released from nests protected on the Texas coast from 2000–14.

released from nests in Texas was in 2012 (Fig. 16), which reflects the highest annual nest total of the same year (Fig. 3).

#### DISCUSSION

Recovery efforts for Kemp's ridley were showing promising signs of success through 2009. A secondary nesting colony had been formed at PAIS, which was one of the objectives of the binational recovery program. Translocation and head-starting efforts helped increase Kemp's ridley nesting in Texas, but most turtles were from the wild stock. The exception is in north Texas, where nesting has been predominated by head-started turtles that were intended to return to Mexico or PAIS to nest. Nesting by head-started turtles contributed to expansion of nesting to north Texas since 2002 when it was first documented. South Texas, including PAIS, continues to be the epicenter of Kemp's ridley nesting in the United States, with about 82% of U.S. nesting occurring there. From 1978 through 2014, 118 Kemp's ridley nests were confirmed in the United States outside of Texas, and more than half of the U.S. nests were found at PAIS (Shaver and Caillouet, 2015).

*Correlation of annual nest numbers in Texas and Mexico, and possible relationship of nesting trends to DWH Oil Spill.*—The annual numbers of nests found in Texas and Mexico from 1978–2014 trended similarly and were highly correlated

(Table 1; Fig. 4). These parallel trends indicate that factors affecting recruitment and survival are impacting the Kemp's ridleys nesting in these two rookeries. Kemp's ridley nesting was increasing exponentially in Mexico and Texas (Márquez et al., 2005; Witzell et al., 2005, 2007; NMFS et al., 2011), but since 2010 (the year of the DWH Oil Spill), that exponential increase has been unexpectedly disrupted, despite continued high nest detection efforts (Caillouet, 2014; Shaver and Caillouet, 2015; Bevan et al., 2016). This sudden reversal in nesting has caused renewed concern about the species' status and interest in identifying factors that might have caused this unexpected change (Caillouet, 2011, 2014; Plotkin and Bernardo, 2014; Gallaway et al., 2016a, 2016b). The DWH Oil Spill released over 4.4 million barrels of oil into the northern Gulf of Mexico (Crone and Tolstoy, 2011). Deaths and impairments of sea turtles and other marine organisms have been linked to the DWH Oil Spill (Antonio et al., 2011; Powers et al., 2013; Incardona et al., 2014; Landers et al., 2014; Etnoyer et al., 2015; Venn-Watson et al., 2015a, 2015b) and possible interactions with other stressors (Carmichael et al., 2012; Whitehead, 2013). Northern Gulf of Mexico waters are important habitat for various life stages of Kemp's ridleys (NMFS et al., 2011; Putman et al., 2013), particularly postnesting adults (Shaver and Rubio, 2008; Shaver et al., 2013), so this species could have been affected through mortality of adults, mortality of other life stages

leading to lower recruitment, sublethal impacts to the turtles, or impacts to their food resources (Campagna et al., 2011). Various other hypotheses regarding the decline have included mortality from fisheries interactions, and reduced fitness and fecundity due to cold winters, reduced freshwater inflow, reduced preferred forage resources (e.g., blue crabs and fisheries by-catch [Shaver, 1991]), density dependence, and combinations of the above (Caillouet, 2014; Plotkin and Bernardo, 2014; Gallaway et al., 2016a, 2016b). Our findings highlight key demographic processes that may be involved and calls for continued research.

*Nesting season.*—Sea turtle nest abundance can be influenced by the dates of first and last nesting, and nesting season duration, which in turn can be affected by water temperatures (Mazaris et al., 2004, 2008; Weishampel et al., 2004, 2010; Pike et al., 2006; Pike, 2009; Lamont and Fujisaki, 2014). We documented Kemp's ridley nesting in Texas from April through mid-July, but the date when the first nest was found was earlier, the date when the last nest was found was later, and the nesting season lasted longer through time. Although most nesting in Tamaulipas occurs during those months, some nesting has also been documented there in March, August, and September (Rostal, 2005; Witzell et al., 2007; J. Peña, pers. comm.). Witzell et al. (2007) hypothesized that the nesting season may have expanded in Mexico with the increases there starting in the mid-1980s; the Texas nesting season expansion may also be related to nesting increases. Water temperatures in the northern Gulf foraging areas during the winter of 2009–10 were among the coldest on record (Gallaway et al., 2016b) and were associated with a delay in the 2010 nesting season in Mexico (Gallaway et al., 2016b) and to a lesser extent in Texas, where the initiation of the nesting season consistently lags behind Mexico by a few weeks. More research is needed regarding potential impacts of sea temperatures and population levels on nesting season for Kemp's ridley.

*Mark-recapture.*—Vital to analyses of nest abundance is examination of current population demographic parameters that drive it, and how these parameters may have changed over time. Mark-recapture is a useful technique to detect if there have been changes in reproductive effort per female within a year (i.e., clutch frequency) or changes in remigration intervals (Hays, 2000;

Broderick et al., 2003; Whiting et al., 2014). All nesting Kemp's ridleys observed in Texas have been measured and tagged since 1995, and with the tag return data we were able to quantify potential changes in remigration interval, clutch frequency, and numbers of remigrants and apparent neophytes nesting in Texas. Tagging has been intermittent in Mexico, particularly when high nesting levels necessitated focus on nest conservation rather than continued mark-recapture studies, so comparable demographic data are lacking for the larger segment of the population that nests there. In the absence of data from Mexico, data from Texas may be useful in understanding trends for all Kemp's ridleys, because there is only one genetic and management unit for this species (Bowen et al. 1991, 1998; Bowen and Karl, 2007; Wallace et al., 2010).

Unfortunately, it was only possible to examine nesting turtles at 55% of the nests found in Texas, which is slightly higher than the 48% observation rate in a study that tagged all individuals seen in Mexico during 1989 (Pritchard, 1990). Robust, saturation mark-recapture tagging studies aim to intercept nearly all turtles that use a particular beach, and document nearly all of their nests during a nesting year (Chaloupka and Musick, 1997). Although high observation rates have been possible for some other species (Richardson et al., 1978, 2006; Lamont et al., 2012, 2014), they may not be possible for Kemp's ridley due to their nesting habits. Kemp's ridleys nest 24 hr a day, although most frequently during the day. Nesting is rapid, and nesting turtles are typically on the beach for only 30–60 min. Because nesting typically occurs in synchronous emergences called *arribadas*, the magnitude of nesting can outpace capacity of mark-recapture personnel. Although there are epicenters of nesting at PAIS in Texas, and at Rancho Nuevo in Mexico, nesting is spread widely from Texas through Veracruz. Based on tag returns from Texas, Kemp's ridleys return to nest on the same or nearby beaches (e.g., North and South Padre islands) about 95% of the time, but nest on distant beaches (e.g., PAIS and Rancho Nuevo) about 5% of the time (Shaver, 2005; Shaver and Caillouet, 2015). Under these conditions, a program that aims to observe nesting turtles at nearly 100% of the nests would require an extremely large labor force and be cost-prohibitive.

Those turtles observed nesting in Texas during a given year are a large subset of the population

nesting there. Although nesting turtles were seen at only 55% of the nests, this likely represents more than 55% of the individuals that nested during a year because Kemp's ridley turtles typically nest multiple times during a nesting year (Pritchard, 1990; NMFS et al., 2011; Frey et al., 2014). Annual minimum, mean, and maximum SCL can be estimated accurately with a 55% observation rate if those observed are a representative subset and sample sizes are sufficiently robust. However, other parameters (i.e., clutch frequency) would be recognized underestimates. Nevertheless, because our observation rate did not vary significantly through time, trends in these parameters over time could indicate changes, even when precision of parameter estimates is reduced by incomplete observation.

*Remigrants and apparent neophytes.*—It appears that recruitment of neophytes into the nesting population declined in recent years, which could have implications for nest abundance. We identified nesting Kemp's ridleys as apparent neophytes or remigrants through examination for tags and tag returns. Tag loss is a confounding variable in sea turtle mark-recapture studies (Chaloupka and Musick, 1997; Ehrhart et al., 2014), but tag retention rates are enhanced by use of PIT tags (as in this study) to improve accuracy of neophyte/remigrant classification (Stokes et al., 2014). It is important to note that turtles identified as neophytes in this study could have nested previously in Texas or elsewhere but were not tagged. However, turtles intercepted at nesting beaches represent a cross-section of the nesting population so changes in percentages across time could reflect changes in the population. From 2000–14, the percentage of turtles examined that were neophytes decreased and, conversely, the percentage that were remigrants increased; these trends continued during 2015 (D. J. Shaver, unpubl. data). A reduced recruitment of neophytes into the nesting population could account for reductions in the numbers of nesting turtles and nests. This decreasing trend of turtles identified as neophytes over time could also reflect a decreasing probability of finding untagged turtles as the tagging project continued, but because we have been tagging since 1995 and Kemp's ridleys mature at approximately 12 yr (NMFS et al., 2011), this factor is likely less significant than for studies of shorter duration on species with longer maturation times. If fewer neophytes are indeed being

recruited into the nesting population, this could be due to increased mortality of large juveniles and/or delayed age to maturity due to reduced forage quantity, quality, or availability. Sea turtle growth rates and both size and age at maturity vary temporally and spatially, and are influenced by environmental and biological factors (Avens et al., 2015). Additionally, the slight but significant increase in mean annual clutch frequency and SCL over time could be due to an increased percentage of remigrant nesting turtles, since both are larger for remigrants than neophytes in some sea turtle species (Márquez, 1994; Lamont et al., 2014; Stokes et al., 2014).

*Remigration interval and clutch frequency.*—Remigration interval and clutch frequency are important factors driving nesting trends and have a large impact on the relationship between the number of nests and the number of adults in the population (Hays, 2000; Heppell et al., 2005; Mazaris et al., 2008; NMFS et al., 2011; Lamont et al., 2012; Neeman et al., 2015; Gallaway et al., 2016a, 2016b). Increased remigration interval or decreased clutch frequency would result in fewer nests being produced, even if there had been no reduction in the adult population. These vital rates are likely variable through time and influenced by environmental factors, population density, and possibly age structure (S. S. Heppell, pers. comm.). Individual Kemp's ridleys must attain a threshold body condition before migration (Stokes et al., 2014), so changes in the remigration interval and clutch frequency could be influenced by colder oceanic temperatures prior to or early in the nesting season or by changes in prey base affecting reproductive condition (Carr and Carr, 1970; Hays, 2000; Hamann et al., 2009; Mazaris et al., 2009; Schofield et al., 2009). For example, a lower portion of adult females may have achieved body condition necessary to support migration and reproduction during the 2010 nesting season due to very cold water temperatures in northern Gulf foraging areas during the winter of 2009–10 (Gallaway et al., 2016b), thereby contributing to the reduction of Kemp's ridley nesting during 2010.

Remigration intervals for this species appear to have increased in recent years, which could have contributed to the decline of nesting observed in recent years. The mean remigration of 1.9 yr in 2008, the first year with good sample size ( $n = 22$ ), was similar to the 2.0-yr remigration interval used in the Kemp's Ridley Recovery Plan (NMFS

et al., 2011) and the 1.8-yr remigration interval found by Witzell et al. (2005) at Rancho Nuevo from 1996–2004. Prior to 2008, sample sizes were small (i.e., 2–9 observations); we did not consider data from these years in our comparisons. All remigration interval estimates for this species have been based on observation of a subset of nesting Kemp's ridleys. All estimates could have been biased by some individual turtles nesting on that or another beach and not being observed, which would result in inaccurately long remigration intervals being calculated for those turtles, and inflating overall remigration interval estimates that included those values. However, this potential source of bias may be minimized because Kemp's ridleys typically nest and can be observed multiple times during the nesting season. It is important to note that long remigration intervals are possible, and two were recently verified for Kemp's ridleys monitored by satellite telemetry that remained in foraging grounds and failed to remigrate for more than 4 yr after nesting at PAIS in 2011, and for more than 3 yr after nesting at PAIS in 2012 (D. J. Shaver, unpubl. data). The mean annual remigration intervals increased steadily from 2008–14, and peaked at 3.3 yr in 2014. Remigration interval increased to 3.5 yr during 2015, which was the longest interval recorded in Texas since the study period began in 2000 (D. J. Shaver, unpubl. data). This coincides with the Gallaway et al. (2016b) population model prediction that remigration intervals for this species increased during recent years. However, there could be differences in remigration intervals between Kemp's ridleys nesting in Texas and Mexico related to the locations of their foraging grounds. Kemp's ridleys nesting in Mexico are a mixture of turtles that overwinter in the southern and northern Gulf, whereas most Texas-nesting turtles migrate to and overwinter in the northern Gulf (Shaver et al., 2013, 2016). Colder temperatures in the foraging grounds of the northern Gulf could have contributed to longer remigration values for Texas-nesting turtles (Schoefield et al., 2009; Lamont and Fujisaki, 2014).

Clutch frequency is another driver of nest abundance, and thus estimating clutch frequency is vital in quantifying abundance of nesting Kemp's ridleys and assessing population trends (Pritchard, 1990). An average clutch frequency of 2.5 nests was used for population modeling in the revised Kemp's Ridley Sea Turtle Recovery Plan (NMFS et al., 2011). Our mean clutch

frequency of 1.3 nests in Texas was similar to the clutch frequency of 1.3–1.5 nests reported from Rancho Nuevo during the 1970s and 1980s (Márquez et al., 1982; Márquez, 1990). However, these are all recognized underestimates of clutch frequency based on mark-recapture tagging where nesting turtles were only observed at about half the nests (Texas 55% [present study]; Mexico 48% [Pritchard, 1990]). Using ultrasonography and plasma testosterone levels, Rostal (2005) estimated that Kemps ridleys actually nested approximately 3.0 times per nesting season at Rancho Nuevo from 1988–90, but this may represent what is theoretically possible rather than what is observed (Frey et al., 2014). Recognizing that our estimates of clutch frequency from tagging are consistently underestimates, because our observation rate has remained constant through time, we may be able to detect changes through time. We found that annual mean clutch frequency increased slightly but significantly through time and this could reflect a larger percentage of remigrants and an aging population (Mortimer and Bresson, 1999; Lamont et al., 2014).

Had nesting turtles been identified for more of the nests in Texas, our estimate of clutch frequency, and the precision of our other vital rates, would have increased. Mitochondrial DNA sequencing combined with nuclear DNA analysis was used to match genotypes for nesters and offspring of unknown parentage in over half of the unassigned nests from 2003–06 (Frey et al., 2014). When genotyping results for all study years become available, these will be linked with mark-recapture studies to increase the data available to quantify demographic parameters for Texas-nesting turtles. Future estimates of clutch frequency and other parameters gathered from capture-mark-recapture methods could also be augmented with the use of other techniques on a random subset of turtles studied throughout the nesting season. Among the techniques that could be useful are ultrasonography, plasma testosterone levels (Rostal, 2005), and perhaps satellite tracking using global positioning system transmitters set with a 24-hr duty cycle (Schroeder et al., 2003; Tucker, 2010).

*Clutch size.*—The mean clutch size for Kemp's ridleys nesting in Texas from 2000–14 was 97 eggs, which mirrors closely the mean clutch size recorded for Rancho Nuevo in 1993–2003 and the clutch size used to estimate population growth in the revised Kemp's Ridley Recovery

Plan (NMFS et al., 2011). However, the Texas mean clutch size was slightly less than the average 100 eggs per nest found at Rancho Nuevo from 1966–92 (Márquez, 1994). Mean clutch size did not change through time from 2000–14 in Texas, but decreased from 1966–92 in Mexico (Márquez, 1994), possibly due to the influx of neophyte nesting turtles as the nesting population increased after the mid-1980s.

*Hatching and emergence success.*—Intensive nest conservation efforts directly contributed to nesting increases recorded from the mid-1980s through 2009 (Caillouet et al., 2014), and continue to be vital to species recovery. To attain high hatching success and hatchling survival of Kemp's ridleys through release, most Texas clutches found were translocated to corrals or an incubation facility to protect them from inundation and washout by high tides and tropical storms, predation, poaching, beach driving, and other threats on the beach. We found a mean emergence success of 83.5% for Texas nests from 2000–14, and a slight increase in mean annual emergence success over time, which likely reflects improvements in egg translocation and care procedures. This emergence success is comparatively high, and hatchlings are protected during release to ensure that they safely enter the sea. Similarly, for decades virtually all Kemp's ridley clutches in Mexico were incubated in corrals. Emergence success for these clutches is estimated to be 67.8%, and all hatchlings are released to the sea (see NMFS et al., 2011). Although most clutches continue to be incubated in corrals in Mexico, with increasing nest numbers it became logistically necessary to allow more nests to incubate *in situ* there starting in 2004 (Gallaway et al., 2016b). Approximately 30% of the nests that incubated *in situ* at Rancho Nuevo from 2009–12 were lost due to erosion, and for the 70% of nests that remained, hatching success averaged about 71% (Bevan et al., 2014). Combining these data, overall hatching success was approximately 51% for the *in situ* nests. For the nests that were not lost to erosion, an estimated 87% of the hatchlings successfully crawled from the nest to the sea (Bevan et al., 2014). Given the recent decline in Kemp's ridley nesting, efforts to maximize recruitment into the population by protecting as many eggs during incubation and hatchlings during release as possible must continue; these techniques were proven successful at aiding with species recovery in the past

(NMFS et al., 2011). Future nesting in Texas and Mexico is highly dependent on hatchling production at these rookeries.

*Conclusions.*—The end of an exponential increase and a subsequent decline in nesting underscore the vital importance of continued protection efforts for Kemp's ridley on the nesting beaches and in the marine environment (Caillouet, 2014; Plotkin and Bernardo, 2014). Our findings of a decline in apparent neophytes and increase in remigration interval of Kemp's ridley could have had a role in the nesting decline, but the factors that caused these demographic changes must be identified. Research into impacts of the DWH Oil Spill on the Kemp's ridley and other factors that may have disrupted the exponential growth in number of nests must continue for many years. We report population vital rate estimates for Kemp's ridley based on the only recent, continuous, long-term mark-recapture effort. However, our limited numbers of nesting turtles available for documentation in Texas, and differences in foraging and migratory habitat use for turtles nesting in Texas vs Mexico may reduce the utility of our findings to draw inferences for the entire population. It is imperative that long-term mark-recapture programs for nesting Kemp's ridley turtles resume in Mexico and continue in Texas. Data collected through these studies are essential to understanding vital rates and conducting population modeling for this endangered species, and may provide insight and information needed to aid with recovery efforts for it.

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