



Embryo deformities and nesting trends in Kemp's ridley sea turtles *Lepidochelys kempii* before and after the *Deepwater Horizon* oil spill

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ABSTRACT: Kemp's ridley sea turtles *Lepidochelys kempii* were disproportionately affected by the *Deepwater Horizon* (DWH) oil spill, which began on 20 April 2010. Embryo deformities were documented in inviable *L. kempii* eggs before (2008–2010) and after (2011–2013) the DWH spill in 2 Texas (USA) nesting areas (Upper Texas Coast and Padre Island National Seashore). Additional nesting trends, including clutch size and hatching success, were also investigated. Total and late-stage embryo deformity prevalence were 1.5 times greater after 2010 than before, but low in all nesting seasons (mean \pm SD: $0.7 \pm 8.5\%$ total; $0.6 \pm 8.0\%$ late-stage) and did not differ between locations. Craniofacial and carapace deformities were the most frequently observed deformity types. Documented nests in both areas declined in 2010 relative to previous years, ending an exponential increase observed beginning in 1995. Clutch size remained consistent before and after the spill. Hatching success averaged $87.0 \pm 33.3\%$ in all years, but no effects from DWH were determined. Collectively, these data represent useful benchmarks against which to judge impacts of future crude oil spills and other catastrophic events.

KEY WORDS: Maternal exposure · Nest success · Craniofacial deformities · Gulf of Mexico · Texas

1. INTRODUCTION

On 20 April 2010, the *Deepwater Horizon*/Mississippi Canyon 252 (DWH) explosion and subsequent 87 d oil leak released 3.19×10^6 barrels (5.07×10^8 l) of oil into the northern Gulf of Mexico (GOM), resulting in the largest marine oil spill in history (DWH NRDA Trustees 2016). At its maximum extent, oil covered 112 115 km² of the GOM and ultimately contaminated the coasts of Louisiana, Mississippi, Alabama, and northern Florida (USA), including adjacent marine waters and wetlands (<https://response.restoration.noaa.gov/erma>). Crude oil released into the marine environment has

grave acute and chronic impacts on many taxa (Peterson et al. 2003), affecting growth rates, reproductive output, and overall fitness of individuals, as well as potentially impacting population dynamics. DWH oil directly and indirectly killed large numbers of organisms and contaminated important foraging and developmental habitats used by many species (Antonio et al. 2011, Henkel et al. 2012, White et al. 2012, Rozas et al. 2014, McDonald et al. 2017). Large amounts of fossil carbon from oil and gas released by the spill have been incorporated into the GOM ecosystem (Mitra et al. 2012, Cherrier et al. 2014, Quintana-Rizzo et al. 2015, Bonisoli-Alquati et al. 2016, Wilson et al. 2016,

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Reich et al. 2017). The northern GOM, which experienced the heaviest impacts, provides key foraging habitat for adult female Kemp's ridley sea turtles *Lepidochelys kempii* that nest along the Texas and Mexico coasts (Seney & Landry 2008, Shaver et al. 2013, Gredzens & Shaver 2020).

L. kempii is predominantly a GOM species that is federally listed (endangered) in the USA (NMFS 2011), Critically Endangered globally (Wibbels & Bevan 2019), and has the smallest geographic nesting range of all marine turtles (Pritchard & Márquez-Millán 1973). Nesting occurs primarily on western GOM beaches, in Tamaulipas and Veracruz, Mexico, and along the Texas coast (Pritchard & Márquez-Millán 1973) with limited nesting on other GOM and US Atlantic beaches (Shaver et al. 2016b). The majority of post-nesting *L. kempii* migrate northeastward along the GOM coast and forage in a shallow (<37 m depth; Shaver & Rubio 2008, Shaver et al. 2016a) coastal corridor from Texas to southwestern Florida, with strong foraging area fidelity (Seney & Landry 2008, Shaver et al. 2013, 2016a, Gredzens & Shaver 2020).

Adult *L. kempii* occur almost exclusively in the GOM, although subadults can inhabit the northwestern Atlantic Ocean along the US Atlantic coast (Lazell 1980, Morreale & Standora 2005). Post-hatchlings and smaller juveniles behave planktonically, congregating in convergence zones with other floating objects, including oil (McDonald et al. 2017). Effects of oil on *L. kempii* are a major concern to all life stages, including nesting females, and most of the turtles killed directly by DWH oiling were juvenile *L. kempii* (McDonald et al. 2017). Direct observation and post-spill modeling of the oil trajectory indicated that many *L. kempii* were exposed (Putman et al. 2015, Wallace et al. 2017). Additionally, 51.5% (n = 17) of adult female *L. kempii*, the majority of which were documented foraging in the northern GOM, showed isotopic signatures indicating oil exposure (Reich et al. 2017). Shortly after DWH exposure, marine turtle mortality rates increased exponentially (Antonio et al. 2011) and marine turtle nest densities decreased significantly on beaches near the spill area (e.g. northern GOM, loggerhead turtles *Caretta caretta*; Lauritsen et al. 2017).

Turtles that survived the initial and acute impacts of the spill may have sustained permanent or temporary physiological injury, experienced difficulty finding food, ingested or inhaled oil, consumed oil-contaminated prey, or moved to other foraging areas (e.g. Milton et al. 2010, Moreno et al. 2013, Beyer et al.

2016). Furthermore, oil exposure in reproductive female turtles can lead to maternal transfer of the lipophilic components of oil and their associated metabolites to eggs, causing embryo deformities and death (Fritts & McGehee 1982, Van Meter et al. 2006, Shigenaka 2010, Field et al. 2017, Zychowski & Godard-Codding 2017). While *L. kempii* rarely experience complete developmental failure of clutches (Backof et al. 2019), oil and related components can have other deleterious effects on turtle nests. In *C. caretta*, crude oil experimentally added to sand above incubating eggs led to significant embryonic mortality and morphological changes (Fritts & McGehee 1982), while crude oil and oil-dispersant (Corexit) exposure led to clinicopathological abnormalities and failure to gain weight in hatchlings (Harms et al. 2019). Similarly, snapping turtle *Chelydra serpentina* eggs exhibited increased embryonic mortality and deformities following exposure to crude oil or oil components *in vitro* (Van Meter et al. 2006) and *in situ*, as did painted turtle eggs *Chrysemys picta* (Bell et al. 2006).

This study investigated potential spill effects on embryo deformities, clutch size, and nest success in *L. kempii* based on statistical comparisons and quantification of data from Texas nesting seasons before (2008–2010) and after (2011–2013) the DWH spill. Research findings on nesting *L. kempii* in Texas are important to the entire nesting population because all individuals constitute 1 genetic stock and a single regional management unit (Wallace et al. 2010). This study was part of the US Department of the Interior Natural Resource Damage Assessment of DWH effects on marine turtles, and serves as a basis for future investigations to prepare for, and respond to, damages caused by future oil spills. Additional information on other aspects of the investigation are described elsewhere (Hooper & Schmitt 2015, Shaver et al. 2016a, Reich et al. 2017).

2. MATERIALS AND METHODS

2.1. Study area

The study area consisted of Kemp's ridley *Lepidochelys kempii* nesting beaches along 2 portions of the Texas coast where long-term monitoring has been conducted: the 105 km length of Padre Island National Seashore (PAIS) and a 100 km section on the Upper Texas Coast (UTC) extending from the southern terminus of Surfside Beach at Brazos Inlet northeastward the length of Bolivar Peninsula to

Rollover Pass (Fig. 1). These areas accounted for 56.5% of US *L. kempii* nests during the study years, 2008–2013 (Shaver et al. 2016b). Systematic patrols were conducted each year to identify, document, and protect *L. kempii* nests. Nests discovered at PAIS and on the UTC were excavated and packed into polystyrene boxes containing sand from the nest sites, then transported to the PAIS laboratory facility for protected incubation, following protection protocols for most nests found on the Texas coast (Shaver & Caillouet 2015). Incubated nests were categorized as those found at PAIS (PAIS-I) and those from the UTC for analyses. Eggs from some nests found at the southern end of PAIS were incubated in fenced beach corrals (PAIS-C). All hatchlings were released to the GOM at PAIS.

2.2. Data collection

Nesting females observed by biologists were examined for flipper tags and tagged with a passive integrated transponder (PIT) and 2 metal tags, if not already present. A biopsy sample was also collected from the trailing edge of one of the rear flippers, if

possible, for genetic analyses. Each turtle was measured for maximum straight, maximum curved (cm; nuchal notch to posterior tip; SCL_{n-t} , CCL_{n-t}), and/or minimum straight carapace length (cm; nuchal notch to posterior notch; SCL_{n-n}) at the first observation of the turtle in the study area each season. Conversion equations to determine SCL_{n-t} from CCL_{n-t} and SCL_{n-n} for individuals missing SCL_{n-t} were developed using linear regression:

$$CCL_{n-t} \text{ to } SCL_{n-t}: SCL_{n-t} = 6.660 + 0.848 CCL_{n-t}; r^2 = 0.88, p < 0.01 \quad (1)$$

$$SCL_{n-n} \text{ to } SCL_{n-t}: SCL_{n-t} = 3.823 + 0.950 SCL_{n-n}; r^2 = 0.94, p < 0.01 \quad (2)$$

SCL_{n-t} was recorded once per year for each female, because there is negligible within-season carapace growth, and measurements were applied to all clutches from each individual within a year. For clutches where a female was not observed nesting, genetic analyses were used to assign unknown clutches to known females (Frey et al. 2014), when possible, and SCL_{n-t} measurements were assigned if they had been taken from the known individual that year.

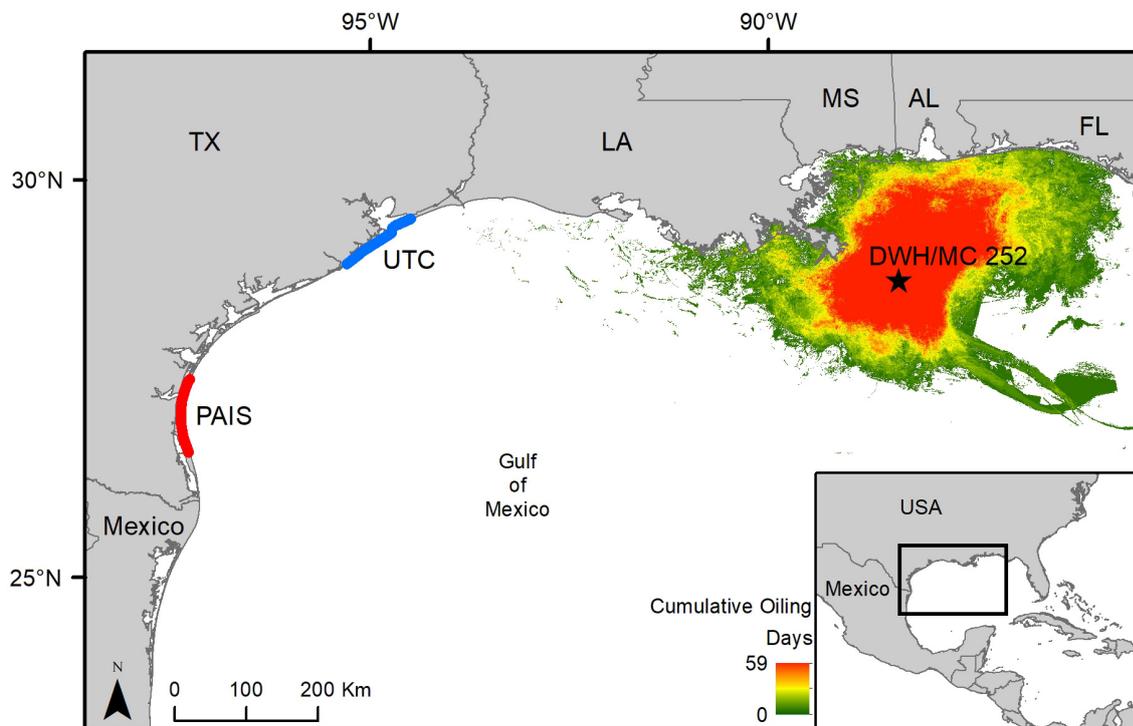


Fig. 1. Northwestern Gulf of Mexico showing study area locations of Kemp's ridley sea turtle *Lepidochelys kempii* nests in Texas (PAIS: Padre Island National Seashore; UTC: Upper Texas Coast), location of the Deepwater Horizon/Mississippi Canyon 252 (DWH/MC 252) wellhead (★), and cumulative days of surface oiling. Surface oiling data represents the Cumulative TCNNA SAR Oiling—Days of Oiling and was obtained from <https://response.restoration.noaa.gov/erma> (accessed 31 March 2020)

At termination of incubation, hatchlings were removed from the sand surface at the first signs of activity, and nest remains, including trapped live hatchlings, were exhumed. All hatchlings were counted, and live hatchlings were released at PAIS. To expedite release of large numbers of hatchlings, limit light exposure, and to follow pre-spill techniques for accurate comparison, live hatchlings were not examined for deformities. Unhatched eggs, including those that were pipped, were salvaged and refrigerated until examination, which occurred within 6 h. Embryos were examined for the presence of grossly visible abnormalities and assigned a developmental stage at mortality (Craatz 1982). Deformities were classified as one of the following: grossly visible craniofacial, carapace, plastron, limb, pigment, and other deformities (e.g. neck and tail, edema, multiple embryos). Tissue samples were collected from 5 embryos from nests where the female was unknown for genetic matching to identified females using the kinship analysis methods described in Frey et al. (2014). The total number of embryos with each type of deformity, along with the total number of deformed embryos and the total number of late-stage (\geq stage 28; Craatz 1982) deformed embryos, were summed for each clutch for analyses and reported as percentages.

2.3. Statistical analyses

We considered 2010 'pre-spill' in all comparisons because *L. kempii* nesting in Texas began on 24 April (4 d after the spill began), and it was assumed that most turtles departed foraging areas before oil spread to these regions (Shaver et al. 2016a, Reich et al. 2017). All analyses were conducted in R v.3.6.3 (R Core Team 2020). All comparative analyses were used to determine any differences pre- and post-DWH (2008–2010 vs. 2011–2013) and between incubation types/locations (PAIS-C, PAIS-I, UTC). Comparisons between specific years were not modeled because year and pre-/post-DWH variables were aliased. Preliminary data exploration was carried out following recommended protocols (Zuur et al. 2010).

A total of 34 irregular clutches (5.2%) ranging from 2 (2010) to 9 (2009) per year were excluded from analyses to eliminate confounding factors. Clutches were excluded if they had been disturbed by predators, inundated by seawater, incubated *in situ* (as opposed to corral or laboratory incubation), were surgically removed from a recently deceased female, or were produced in captivity by oxytocin administra-

tion. For the 6 yr period, 650 clutches were included in analyses. Two additional clutches were removed from analysis of deformity rates because they had 100% developmental failure and thus no embryos were examined.

Deformity rates (total and late-stage) for 519 clutches, where the identity of the female was known through direct observation or genetic assignment, were evaluated using generalized linear mixed models (GLMMs). Deformity rates were modeled as the proportion of 'successes' (deformed embryos/hatchlings) and the proportion of 'failures' (normal embryos/hatchlings). Differences between specific deformity types were not analyzed, as some deformities occurred at such low frequencies that analyses could not be completed. Preliminary statistical testing indicated over-dispersion and zero-inflation of the data. Due to these factors, zero-inflated binomial GLMMs with a logit link function were used to analyze deformity rates, which incorporated a zero-model to account for excess zeroes and a binomial-model to determine the prevalence of the response. The proportions of deformities were modeled as functions of the fixed main covariates incubation type/location (categorical with 3 levels) and pre-/post-DWH (categorical with 2 levels) with nest day (continuous) as a nuisance variable. Maximum SCL_{n-t} was not included as a covariate as it was not correlated with any deformity types. Turtle identity was included as a random effect to account for non-independence of clutches from known females (i.e. multiple clutches assigned to a specific female within and between years).

Using linear regression, nesting data indicated the expected positive relationship between clutch size and SCL_{n-t} ($r^2 = 0.13$, $F_{1,464} = 70.65$, $p < 0.001$) (Fig. 2) (Witzell et al. 2005). A weaker negative relationship between clutch size and nest date (day of the nesting season, beginning with detection of the first nest in each study area each year) was also evident, with clutch size decreasing slightly as the nesting season progressed ($r^2 = 0.02$, $F_{1,647} = 13.15$, $p < 0.001$) (Fig. 2). There was no significant interaction between SCL_{n-t} and nest date. Consequently, comparisons of clutch size between study locations and pre-/post-DWH required accounting for both nest date and SCL_{n-t} . Clutch size was evaluated using a linear mixed model (LMM) and included data from 466 clutches from known females with associated SCL_{n-t} measurements. Nest data without corresponding SCL_{n-t} measurements ($n = 184$) were excluded from clutch size analyses, as SCL_{n-t} was found to have a positive relationship with clutch size. Clutch size was modeled as a function of the fixed covariates pre-/post-

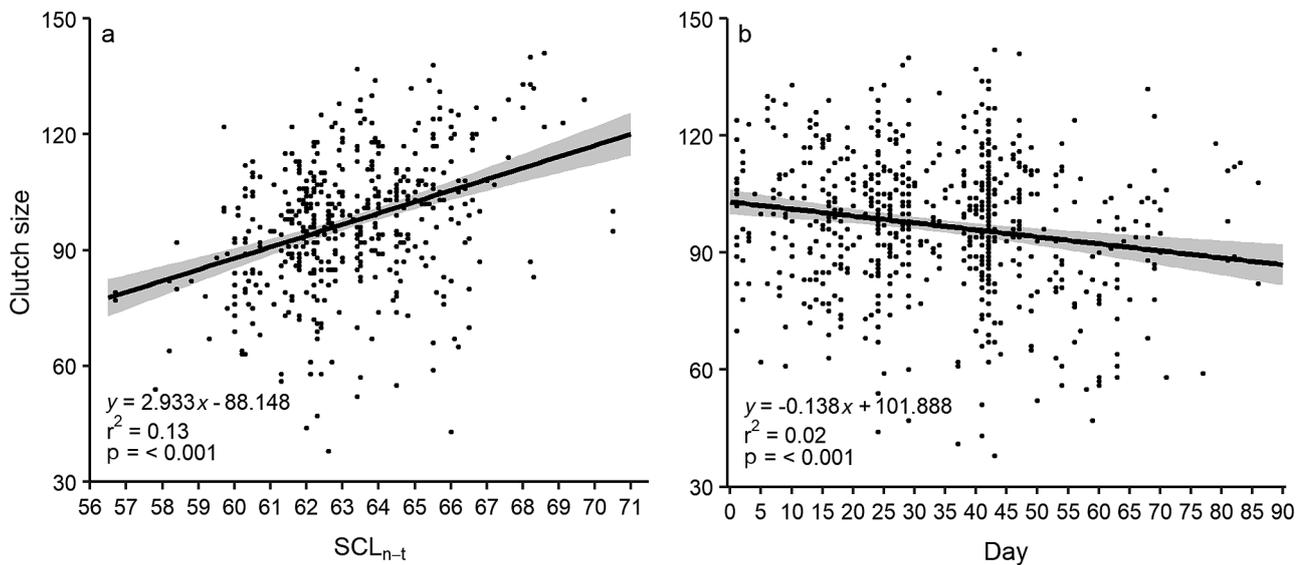


Fig. 2. Overall linear regressions describing relationship between clutch size and (a) maximum straight carapace length (SCL_{n-t}) and (b) nest day of Kemp's ridley sea turtles *Lepidochelys kempii* between 2008 and 2013; 95% confidence intervals shaded in gray. Clutch 2012-97, which contained only 6 eggs, was excluded from analyses

DWH, incubation type/location, SCL_{n-t} (continuous), and nest date (continuous) with turtle identity included as a random effect.

Initial analyses indicated hatching success to be highly variable within and between years, time periods, and locations. Due to these factors, it was not possible to successfully model hatching success to fit the data to determine any effects post-DWH or between incubation types/locations. Therefore, hatching success is presented as observational data only.

LMMs were conducted using the 'lme4' package (Bates et al. 2015) and evaluated using standard methods (Zuur et al. 2010). GLMMs were conducted using the 'glmmTMB' package (Brooks et al. 2017) and were evaluated using the 'DHARMA' package (Hartig 2020). Models were fit to the data by testing the significance of each variable at each step and extracting non-significant terms (backwards step-wise) from the maximal models, using Akaike's information criterion for comparisons, until the most parsimonious (i.e. minimally adequate) model was obtained for each response variable (Crawley 2015). A significance level of $\alpha = 0.05$ was used to judge the significance of all statistical tests. Interaction terms of fixed and nuisance covariates were included in maximal models (Crawley 2015), where appropriate (Zuur et al. 2010). Nakagawa's r^2 was used to determine the amount of variance explained by only the fixed (marginal r^2) and both the fixed and random (conditional r^2) effects of each final mixed model using the 'performance' package (Nakagawa & Schielzeth 2013, Nakagawa et al. 2017, Lüdecke et

al. 2020). Only the main effect means (incubation type/location and pre-/post-DWH) are presented, with the focus on before/after comparisons. All data are reported as means \pm SD.

3. RESULTS

3.1. Yearly nesting activity

A total of 1094 *Lepidochelys kempii* nests were located in Texas during 2008–2013. Of these, 684 (62.5%) were within the study area (594 [87%] at PAIS, 90 [13%] UTC) ranging from 53% in 2008 to 66% in 2011, consistent with 1995–2010 trends, when nesting increased in Texas (Shaver et al. 2016b). Annual nest totals ranged from 141 (2010) to 209 (2012) for all of Texas and from 88 (2010) to 132 (2011) for the study area.

Data were analyzed after exclusion of irregular clutches. Females were directly examined for size and tags at 413 of the 650 nests included in the analyses (63.5%) during 2008–2013 (Table 1). UTC females were directly examined approximately half as often as PAIS females. An additional 108 clutches were assigned to known females using genetic analyses (Frey et al. 2014). Over the 6 yr study, using tag numbers and genetic analyses, 199 females were documented nesting only once during a nesting season, 122 were documented twice, and 26 were documented 3 times for a total of 521 clutches from 240 unique individuals (Table 1); 129 clutches were not

Table 1. Annual numbers of Kemp's ridley sea turtle *Lepidochelys kempii* nests found in Texas, within Padre Island National Seashore (PAIS), and on the Upper Texas Coast (UTC) study areas (SA) from 2008–2013, excluding nests not suitable for analysis. UTC-I: nests located on the UTC, incubated in the laboratory facility; PAIS-C: nests at PAIS, incubated in corrals; PAIS-I: nests at PAIS, incubated in the laboratory facility; total SA: nests combined for the 2 study areas; total TX: total number of nests in Texas, including those excluded from analysis; females in study areas: number of females directly observed or genetically matched to nests within each year or time period; nests per female: SA nests with a female identified divided by the number of females; nests with female: nests where the female was identified either by observation or genetic matching; ND: not determined; NA: not applicable

| Year (no. excluded), location/parameter | All nests | Nests with female | Year (no. excluded), location/parameter | All nests | Nests with female |
|--|------------------|--|--|----------------------|----------------------|
| 2008 (5) | | | 2011 (5) | | |
| UTC-I | 13 | 8 | UTC-I | 18 | 12 |
| PAIS-C | 11 | 7 | PAIS-C | 37 | 30 |
| PAIS-I | 80 | 68 | PAIS-I | 77 | 69 |
| Total SA | 104 | 83 | Total SA | 132 | 111 |
| Total TX | 195 ^a | ND | Total TX | 199 ^a | ND |
| Females in study areas | NA | 52 | Females in study areas | NA | 69 |
| Nests per female | NA | 1.6 ± 0.7 | Nests per female | NA | 1.6 ± 0.6 |
| 2009 (9) | | | 2012 (7) | | |
| UTC-I | 7 | 2 | UTC-I | 12 | 8 |
| PAIS-C | 23 | 18 | PAIS-C | 34 | 29 |
| PAIS-I | 89 | 78 | PAIS-I | 66 | 54 |
| Total SA | 119 | 98 | Total SA | 112 | 91 |
| Total TX | 197 ^a | ND | Total TX | 209 ^a | ND |
| Females in study areas | NA | 68 | Females in study areas | NA | 58 |
| Nests per female | NA | 1.2 ± 0.6 | Nests per female | NA | 1.6 ± 0.7 |
| 2010 (2) | | | 2013 (6) | | |
| UTC-I | 15 | 8 | UTC-I | 13 | 5 |
| PAIS-C | 21 | 17 | PAIS-C | 27 | 24 |
| PAIS-I | 52 | 41 | PAIS-I | 55 | 43 |
| Total SA | 88 | 66 | Total SA | 95 | 72 |
| Total TX | 141 ^a | ND | Total TX | 153 ^a | ND |
| Females in study areas | NA | 47 | Females in study areas | NA | 53 |
| Nests per female | NA | 1.4 ± 0.5 | Nests per female | NA | 1.4 ± 0.6 |
| | | Year (no. excluded), location/parameter | All nests | Nests with female | |
| | | Six-year totals (34) | | | |
| | | UTC-I | 78 | 43 | |
| | | PAIS-C | 153 | 125 | |
| | | PAIS-I | 419 | 353 | |
| | | Total SA | 650 | 521 | |
| | | Total TX | 1094 ^a | ND | |
| | | Females in study areas | NA | 347 | |
| | | Nests per female | NA | 1.5 ± 0.6 | |

^aAll nests documented for Texas each year, with no exclusions

assigned to a female. These unassigned nests were laid by unobserved nesting females who may have been first time nesters, turtles that nested previously in the study area but evaded detection, or turtles that have nested in the study area for the first time but nested elsewhere previously, thus identity could not be assigned. These clutches were not included in the mixed models. Unique females documented nesting in each year ranged from 47 (2010) to 69 (2011) (Table 1). No individuals were observed to have

switched between PAIS and UTC to nest within a nesting season. Turtles were documented to nest an average of 1.5 ± 0.6 times yr^{-1} , with the same rate before and after the spill (1.5 ± 0.6 nests yr^{-1} from 2008–2010 and 2011–2013) (Table 1).

Maximum SCL_{n-t} measurements were available for females of 459 clutches and estimated for an additional 7 clutches ($n = 4 \text{ CCL}_{n-t}$; $n = 3 \text{ SCL}_{n-t}$), resulting in a total of 466 clutches from 347 measured females. Average size was 63.1 ± 2.1 cm SCL_{n-t} with

no apparent differences between study areas (PAIS: 63.2 ± 2.1 cm; UTC: 62.5 ± 1.6 cm) or pre-/post-DWH (2008–2010: 63.0 ± 2.1 cm; 2011–2013: 63.2 ± 2.1 cm). The total number of measured individuals is greater than 240, as known individuals returned to nest in more than one season, with new measurements obtained each year they were seen.

3.2. Embryo deformities

Two clutches from UTC, laid by the same female in 2010, had 100% developmental failure and were not included in deformity analyses. After the exclusion of these 2 clutches, 648 clutches were analyzed for general summary statistics and a total of 459 deformed dead embryos were observed in 241 clutches (37.2%) at an overall rate of $0.7 \pm 8.5\%$ clutch⁻¹ (Table 2). The majority of deformities were late-stage (developmental stage 28 or later; overall $0.6 \pm 8.0\%$ nest⁻¹). Nine of the clutches with the greatest percentages of deformed embryos (>5%, n = 11) were from 2011 or 2012, while 2 were from 2009. All clutches with elevated deformity rates, except one, were laid at PAIS.

From the 519 clutches laid by known females, excluding the 2 failed clutches, there were no significant interactions between variables, and incubation/location type and nest date were also non-significant and were removed from the models to create the minimally adequate GLMMs which included pre-/post DWH as the main effect, and turtle identity as a random effect. Final models indicated a 1.5 times higher rate of total number of deformities and of total late-stage deformities in *L. kempii* clutches post-DWH (total deformities: pre-DWH = $0.8 \pm 0.1\%$, post-DWH

= $1.15 \pm 0.2\%$, $p < 0.01$; late-stage deformities: pre-DWH = $0.6 \pm 0.1\%$, post-DWH = $0.9 \pm 0.2\%$, $p < 0.01$) (Fig. 3, Table 3). Inclusion of the random effect increased the explanatory power of each GLMM (total deformities: marginal $r^2 = 0.01$, conditional $r^2 = 0.14$; late-stage deformities: marginal $r^2 = 0.01$, conditional $r^2 = 0.18$), but model explanation of the variability was low overall.

Craniofacial and carapace deformities were the most frequently recorded deformity types; a total of 215 embryos with craniofacial deformities and 174 with carapace deformities were observed, which represented a prevalence of 0.3 ± 5.8 and $0.3 \pm 5.2\%$, respectively, across all years and locations (Fig. 4). Other types of deformities were detected less frequently (pigment, n = 86, $0.1 \pm 3.7\%$; limb, n = 62, $0.1 \pm 3.1\%$; other, n = 62, $0.1 \pm 3.1\%$; and plastron, n = 51, $0.1 \pm 2.8\%$; Fig. 4). All types of deformities occurred more frequently in clutches in 2011–2013 than in 2008–2010 (Table 2).

3.3. Clutch size and hatching success

The 650 clutches included in general summary statistical analyses contained 63 138 eggs during 2008–2013, of which 55 140 hatched (87.3%) and from which 54 981 hatchlings (87.1%) emerged and were released (Table 4). Over the 6 yr study, $99.7 \pm 5.4\%$ of the turtles that hatched survived and were released. For the 466 clutches from known females with associated SCL_{n-t} measurements, clutch size did not significantly differ pre- and post-DWH ($p = 0.28$) but did differ between locations, with PAIS-I and PAIS-C having lower average clutch sizes (PAIS-I: $p < 0.01$;

Table 2. Annual, total, and pre- (2008–2010)/post- (2011–2013) *Deepwater Horizon* numbers of clutches included in the 2008–2013 Kemp's ridley *Lepidochelys kempii* analysis of dead embryos with deformities after exclusion of all disturbed, abnormal, and failed clutches (n = 36). Late-stage embryos: deformities in embryos stage 28 and higher; 'other' deformity types include neck and tail, edema, multiple embryos and other unclassified deformities. Values in parentheses are percentages of total clutches for the category

| Year | Clutches | Deformities | | | | | | | |
|-----------|----------|---------------|----------------|------------------|--------------|--------------|-----------|-------------|-----------|
| | | All types (%) | Late-stage (%) | Craniofacial (%) | Carapace (%) | Plastron (%) | Limb (%) | Pigment (%) | Other (%) |
| 2008 | 104 | 24 (23.1) | 23 (22.1) | 9 (8.7) | 5 (4.8) | 1 (1.0) | 6 (5.8) | 4 (3.8) | 8 (7.7) |
| 2009 | 119 | 46 (38.7) | 44 (37.0) | 24 (20.2) | 18 (15.1) | 2 (1.7) | 6 (5.0) | 9 (7.6) | 15 (12.6) |
| 2010 | 86 | 28 (32.6) | 25 (29.1) | 17 (19.8) | 4 (4.7) | 1 (1.2) | 3 (3.5) | 7 (8.1) | 1 (1.2) |
| 2011 | 132 | 48 (36.4) | 47 (35.6) | 34 (25.8) | 25 (18.9) | 12 (9.1) | 11 (8.3) | 15 (11.4) | 7 (5.3) |
| 2012 | 112 | 56 (50.0) | 54 (48.2) | 38 (33.9) | 39 (34.8) | 14 (12.5) | 13 (11.6) | 15 (13.4) | 11 (9.8) |
| 2013 | 95 | 39 (41.1) | 37 (38.9) | 24 (25.3) | 20 (21.1) | 14 (14.7) | 16 (16.8) | 15 (15.8) | 12 (12.6) |
| Total | 648 | 241 (37.2) | 230 (35.5) | 146 (22.5) | 111 (17.1) | 44 (6.8) | 55 (8.5) | 65 (10.0) | 54 (8.3) |
| 2008–2010 | 309 | 98 (31.7) | 92 (29.8) | 50 (16.2) | 27 (8.7) | 4 (1.3) | 15 (4.9) | 20 (6.5) | 24 (7.8) |
| 2011–2013 | 339 | 143 (42.2) | 138 (40.7) | 96 (28.3) | 84 (24.8) | 40 (11.8) | 40 (11.8) | 45 (13.3) | 30 (8.8) |

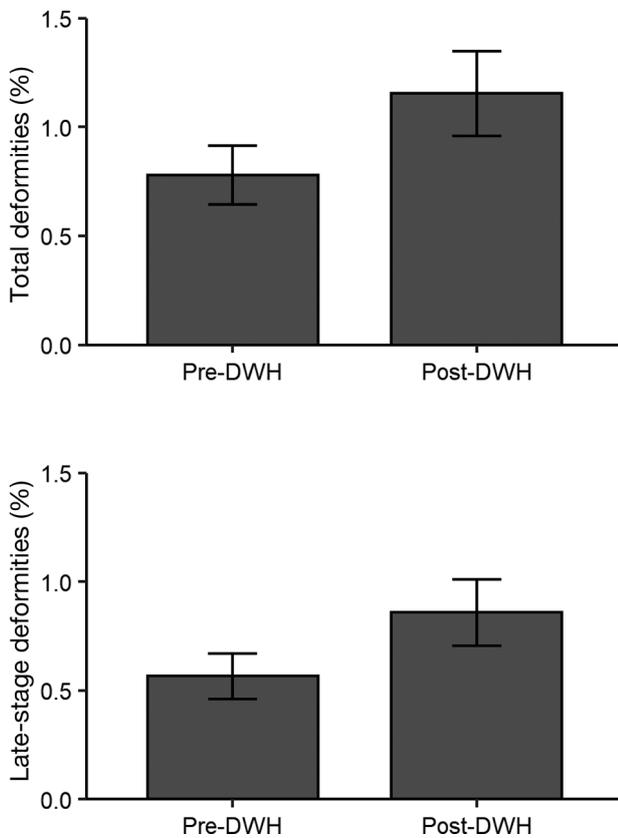


Fig. 3. Zero-inflated generalized linear mixed model results of the proportion of total and late-stage deformities of embryos found in *Lepidochelys kempii* clutches laid along the Texas, USA, coast pre- (2008–2010) and post- (2011–2013) *Deepwater Horizon* (DWH). Error bars: ± 1 SE

PAIS-C: $p < 0.05$) (Fig. 5, Table 3). Inclusion of the random effect increased the overall explanatory power of the LMM (marginal $r^2 = 0.20$, conditional $r^2 = 0.41$). Overall hatching success was $87.3 \pm 33.3\%$ for the 6 yr period, $87.8 \pm 32.7\%$ pre-DWH, and $86.9 \pm 33.8\%$ post-DWH. Hatching success was highly variable among nests from different locations within the study area, with higher rates of success for PAIS-I ($88.4 \pm 32.0\%$) and PAIS-C ($91.1 \pm 28.5\%$) than UTC ($74.5 \pm 43.6\%$).

4. DISCUSSION

International conservation efforts implemented since the mid-1970s resulted in an exponential increase of *Lepidochelys kempii* nests documented each year from 1999–2009 (Caillouet 2011, Gallaway et al. 2016a,b, Shaver et al. 2016b, Wibbels & Bevan 2016). However, nest numbers in Mexico and Texas, which are highly correlated and represent portions of the same nesting population (Shaver et al. 2016b), decreased 37% in 2010 relative to 2009, as did the number of hatchlings released (Crowder & Heppell 2011), representing a major departure from trends in previous years. Nest numbers remained lower than predicted after the DWH spill (Bevan et al. 2016, Gallaway et al. 2016b, Shaver et al. 2016b) and did not begin to increase again until 2016. Nesting has not resumed the exponential increase observed prior to DWH, causing further concern for the sta-

Table 3. Results of generalized and general linear mixed effects models (GLMM/LMM) of deformity rates and clutch size in *Lepidochelys kempii* clutches before (2008–2010) and after (2011–2013) the *Deepwater Horizon* (DWH) oil spill. Deformity rates were modeled using a zero-inflated binomial GLMM with logit link; clutch size was modeled using an LMM. PAIS-I: Padre Island National Seashore incubation facility; PAIS-C: Padre Island National Seashore corral; SCL_{n-t} : straight carapace length, nuchal notch to posterior tip (cm)

| Model | Variable | Unstandardized coefficients | | z | p |
|--------------------------------------|----------------------|-----------------------------|--------|---------|--------|
| | | Estimate | SE | | |
| Total deformities (conditional) | Intercept | -4.846 | 0.174 | -27.909 | <0.001 |
| | Pre-/post-DWH [post] | 0.396 | 0.145 | 2.732 | <0.01 |
| Total deformities (zero) | Intercept | -0.558 | 0.244 | -2.288 | <0.05 |
| Late-stage deformities (conditional) | Intercept | -5.170 | 0.186 | -27.874 | <0.001 |
| | Pre-/post-DWH [post] | 0.420 | 0.148 | 2.836 | <0.01 |
| Late-stage deformities (zero) | Intercept | -0.935 | 0.332 | -2.812 | <0.01 |
| Clutch size | Intercept | -79.747 | 25.074 | -3.180 | <0.01 |
| | Pre-/post-DWH [post] | 1.584 | 1.472 | 1.076 | 0.283 |
| | Location [PAIS-C] | -7.482 | 3.673 | -2.037 | <0.05 |
| | Location [PAIS-I] | -9.930 | 3.444 | -2.884 | <0.01 |
| | SCL_{n-t} | 3.022 | 0.398 | 7.593 | <0.001 |
| | Nest date | -0.204 | 0.041 | -5.040 | <0.001 |

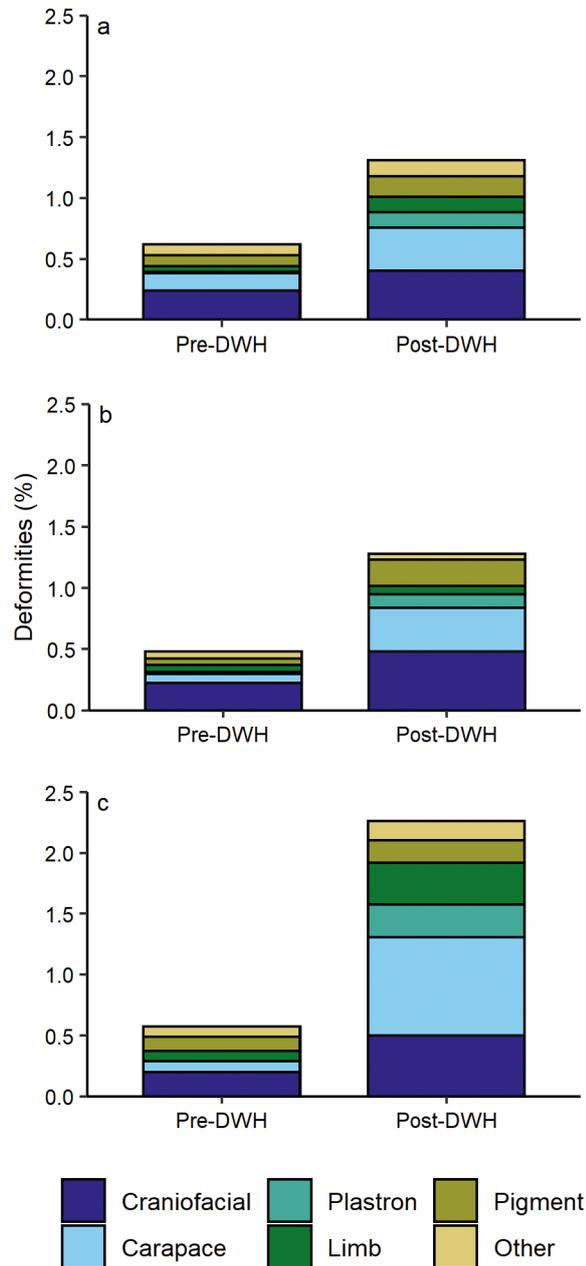


Fig. 4. Mean prevalence (un-weighted proportional means) of embryo deformity types (as percentages of clutch size) in Kemp's ridley sea turtle *Lepidochelys kempii* clutches, pre- (2008–2010) and post- (2011–2013) *Deepwater Horizon* (DWH) at (a) Padre Island National Seashore incubation facility (PAIS-I); (b) Padre Island National Seashore corral (PAIS-C), and (c) upper Texas coast (UTC)

tus of this species (Gallaway et al. 2016b, Caillouet et al. 2018).

Most *L. kempii* nesting occurs on the Gulf coast of Mexico in Tamaulipas and Veracruz and to a lesser extent in Texas (Shaver et al. 2016b). Nearshore waters of the northern Gulf, the same geographic area

affected by the DWH oil spill, provide particularly important foraging and migratory habitat for *L. kempii* that migrate from nesting beaches in Texas and Mexico (Shaver & Rubio 2008, Shaver et al. 2013, 2016a, Putman et al. 2015, Wallace et al. 2017, Gredzens & Shaver 2020). Impacts from the DWH oil spill, if present, may have directly affected nesting females (oiling or disturbance) or indirectly affected them via ingestion of oil or related compounds from the water column or dietary sources (Zychowski & Godard-Codding 2017). Anthropogenic activities post-DWH, such as increased boat traffic during clean-up, may also have had detrimental effects on marine turtle populations (Lauritsen et al. 2017). It is unknown if oil contamination of the foraging grounds affected reproductive success and, ultimately, the observed slowed population recovery.

Deformity rates were higher in examined *L. kempii* embryos post-DWH. Statistical models explained a comparatively small proportion of the total variation in the data, thus indicating that factors not incorporated into the models are likely important. Possible confounding variables could be error introduced by embryo deformity examiners and/or a possible increased scrutiny of embryo examination after the oil spill due to awareness of the study. Future studies should work to mitigate these types of confounding factors. For this study, live hatchlings were not examined for deformities in order to protect them from exposure to white light and allow for quick release. Analysis of the data based only on females observed and examined while nesting or genetically matched to clutches indicates that differences between or among nests made by the same turtle account for substantially more of the total variation for some of the variables analyzed. Deformed embryo prevalence was low overall and highly variable ($0.7 \pm 8.5\%$), indicating probable low population-level impacts. In comparison, turtle embryo deformities from John Heinz National Wildlife Refuge, which is highly contaminated by multiple sources, ranged from 13–71% annually in 2 freshwater species, *Chelydra serpentina* and *Chrysemys picta* (Bell et al. 2006). Frequency of malformations for marine turtle eggs has also been reported in other species of marine turtles, for both *in situ* and relocated nests, ranging from 0.2–26.0%, with high variability between species and locations (Bárcenas-Ibarra et al. 2015). Embryo malformation rates for the most closely related species of marine turtle, the olive ridley *Lepidochelys olivacea*, are relatively high (1–2%) when compared to other species (Bárcenas-Ibarra et al. 2015).

Annual clutch size and frequency were monitored for changes after the spill, as fecundity is critical to

Table 4. Annual, total, and pre- (2008–2010)/post- (2011–2013) *Deepwater Horizon* clutch size and nest success for Kemp's ridley *Lepidochelys kempii* within the study area after exclusion of all disturbed and abnormal clutches ($n = 34$). Values in parentheses are percentages of total eggs/hatchlings for the category

| Year | Total clutches | Total eggs (%) | Hatched eggs (%) | Unhatched eggs (%) | Hatchlings released (%) |
|-----------|----------------|----------------|------------------|--------------------|-------------------------|
| 2008 | 104 | 10 117 (16.0) | 9207 (91.0) | 910 (9.0) | 9196 (90.9) |
| 2009 | 119 | 11 210 (17.8) | 9668 (86.2) | 1542 (13.8) | 9644 (86.0) |
| 2010 | 88 | 8581 (13.6) | 7399 (86.2) | 1182 (13.8) | 7385 (86.1) |
| 2011 | 132 | 13 173 (20.9) | 11 421 (86.7) | 1752 (13.3) | 11 378 (86.4) |
| 2012 | 112 | 10 898 (17.3) | 9468 (86.9) | 1430 (13.1) | 9438 (86.6) |
| 2013 | 95 | 9159 (14.5) | 7977 (87.1) | 1182 (12.9) | 7940 (86.7) |
| Total | 650 | 63 138 | 55 140 (87.3) | 7998 (12.7) | 54 981 (87.1) |
| 2008–2010 | 311 | 29 908 (47.4) | 26 274 (87.8) | 3634 (12.2) | 26 225 (87.7) |
| 2011–2013 | 339 | 33 230 (52.6) | 28 866 (86.9) | 4364 (13.1) | 28 756 (86.5) |

long-term population dynamics. For grouped years, 2008–2010 (pre-DWH) vs. 2011–2013 (post-DWH), clutch size was not significantly different, but did differ between study locations after accounting for turtle size and nest date, with larger clutches found on the UTC. Differences in clutch size between locations are likely the result of more nesting at PAIS paired with increased patrol effort there late in the nesting season (August–September) (Shaver et al. 2016b). Analysis indicated that nesting day may affect clutch size, with smaller clutches later in the season (Fig. 2b). Other factors may also contribute, as the explanatory power of the model was low. In addition, there may be other unexplained factors as to why UTC clutch sizes are larger, such as mean individual age or health or the closer proximity of the UTC to important foraging areas (Shaver et al. 2013, 2016a).

Over 36 yr (1978–2014), annual mean clutch size did not vary greatly for *L. kempii* nesting in Texas (Shaver et al. 2016b). Considered together, the number of nests detected per known female was the same in 2011–2013 (1.5 ± 0.6) and 2008–2010 (1.5 ± 0.6). However, identified turtles undoubtedly made some of the nests laid by unidentified females, indicating that the number of nests per female is lower than the estimated total at $1.8 \text{ nests yr}^{-1}$ (Frey et al. 2014, Shaver et al. 2016b).

Hatching success for *L. kempii* nests in the study areas was monitored for changes after DWH. However, no significant differences in hatching success between 2008–2010 and 2011–2013 were found due to high variability in the data. Hatch success is very complex and is impacted by many factors (e.g. nest temperature, moisture, sand quality, genetics, health

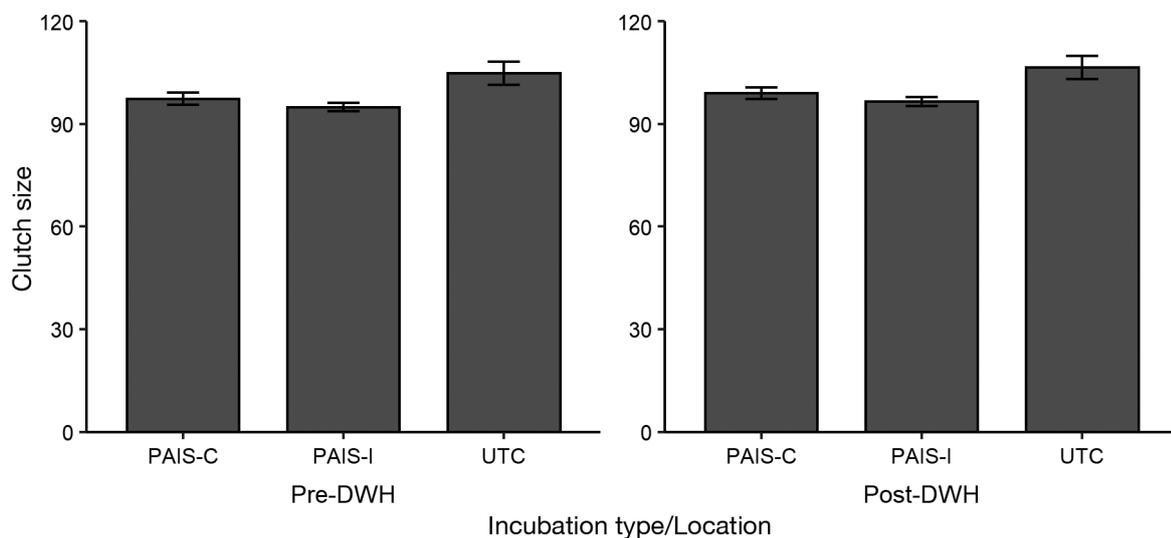


Fig. 5. Linear mixed model results of Kemp's ridley sea turtle *Lepidochelys kempii* clutch size pre- (2008–2010) and post- (2011–2013) *Deepwater Horizon* (DWH) divided by incubation type and location. PAIS-C: Padre Island National Seashore coral; PAIS-I: Padre Island National Seashore incubation facility; UTC: Upper Texas coast incubated at PAIS-I. Error bars: ± 1 SE

status of the nesting female), some of which are difficult to quantify for the purpose of analysis. For example, individual *L. kempii* experience complete developmental failure of clutches on rare occasions for unknown reasons during a nesting season (Backof et al. 2019). For these reasons, this parameter may be of limited benefit in future studies examining short-term impacts of oil spills, unless the impacts are profound. Long-term impacts of persistent environmental exposure (Peterson et al. 2003), ontogenetic effects (Bell et al. 2006), or latency factors may delay detectability for many years.

The timing of the spill likely mitigated impacts to *L. kempii* during 2010, as females nesting during that season migrated away from the oiled habitat to nesting grounds prior to the spill (Shaver et al. 2016a). Data from satellite-tracked adult nesting females and stable isotope samples indicated that 51.5% of the *L. kempii* in the northern GOM may have been exposed to DWH oil in 2010–2012 (Reich et al. 2017), consistent with other reports of marine turtle interactions with oil in the northern GOM (McDonald et al. 2017, Wallace et al. 2017). These assumptions are further supported by the fact that chemical analyses of eggs and embryos salvaged from 2010–2012 nests contained no detectable, or extremely low, concentrations of oil metabolites (Hooper & Schmitt 2015). These observations do not preclude the possible involvement of the spill in the lower than expected nest numbers in Texas and Mexico during 2011–2015 (Crowder & Heppell 2011, Shaver et al. 2016b) (i.e. in addition to direct mortalities of adult turtles, oil-affected turtles that survived the spill may not have migrated and/or nested).

Observations of nesting turtles and nest success represent only the beginning and the end of the marine turtle reproductive cycle. Tracking data from 2010–2013 indicate that many nesting female *L. kempii* traveled in the oiled area after nesting in Texas (Shaver et al. 2016a, Gredzens & Shaver 2020), and immature turtles exposed to oil from the DWH spill and the progeny of exposed adults will not mature for many years. Impacts observed in this study remain low but could be drastically different if a similar environmental disaster occurred closer to the main nesting areas (Lauritsen et al. 2017), where significant numbers of oil and gas platforms overlap with critical habitat (Shaver et al. 2017). There is significant potential for future catastrophic oil releases within critical foraging habitat and *L. kempii* nesting beaches (Shaver et al. 2017). Continued evaluation of data from nesting beaches (i.e. nest numbers, nest success, remigration intervals, growth rates, and re-

cruitment) is necessary to provide evidence of whether oil contamination at the foraging grounds affects reproductive success and, ultimately, population recovery. Data and methods reported here represent useful benchmarks against which to judge impacts to marine turtles by future oil spills and can serve as a basis for future investigations to prepare for, and respond to, damages caused.

Acknowledgements. This study was supported by the US Department of the Interior, Natural Resource Damage Assessment and Restoration Program; the National Park Service; and the US Geological Survey (USGS). Field activities at PAIS were coordinated by the PAIS Sea Turtle Science and Recovery Program and at UTC by the Texas A&M University — Galveston Trophic Ecology and Sea Turtle Research Laboratory. Sampling at PAIS was authorized under US Fish and Wildlife Service (USFWS) Permit TE840727-3 and Texas Parks and Wildlife Department (TPWD) Scientific Permit SPR-0190-122 and performed in accordance with Institutional Animal Care Protocol NPS IACUC 2011-15. UTC sampling was conducted under and in accordance with IACUC AUP 2010-213 and authorized under USFWS permit TE7761 and TPWD permit SPR-0212-028. M. Hooper (USGS), T. Shearer (USFWS), and S. Finger (USGS) facilitated many aspects of the investigation. R. Tillitt (USGS) guided initial laboratory technique development and assisted in the field and with data management. Additional field and laboratory assistance were provided by C. Iseton and K. Reich. We greatly appreciate comments on earlier versions of the manuscript provided by K. M. Hart (USGS), T. Backof (NPS), M. Tiwari, NOAA, the editors, and 3 anonymous reviewers. Some of the work by C.J.S. was done while serving as a volunteer with the USGS. Any use of trade, product, or firm names is for descriptive purposes only and does not constitute endorsement by the US Government.

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Editorial responsibility: Bryan P. Wallace,
Fort Collins, Colorado, USA
Reviewed by: 3 anonymous referees

Submitted: September 11, 2020
Accepted: December 18, 2020
Proofs received from author(s): March 16, 2021