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Comparison of beach temperatures in the nesting range of Kemp's ridley sea turtles in the Gulf of Mexico, Mexico and USA

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ABSTRACT: Rising environmental temperatures associated with climate change can adversely affect sea turtles whose hatchling sex determination is temperature-dependent. One hypothetical response of sea turtles to near-future elevated temperatures is a shift in nesting distribution to maintain suitable thermal conditions. Assessing sea turtle responses to climate warming involves evaluating (1) how temperatures will be altered, (2) a species' capacity to respond to changes, and (3) whether responses can mitigate the impacts of warming. We evaluated sand temperatures across nesting habitat of the Critically Endangered Kemp's ridley sea turtle *Lepidochelys kempii* in the western Gulf of Mexico. Most nesting now occurs on a 30 km stretch of beach in Tamaulipas, Mexico, but was historically more widely distributed. Applying conservative projections, we assessed whether a shift in the epicenter of nesting to the northern extent of the present distribution would maintain incubation temperatures below lethal levels and suitable to produce hatchlings of both sexes. Coupling temperature measurements with known impacts of temperature on the reproductive physiology of *L. kempii*, we predict that northern beaches will initially support the production of mixed sex ratios. However, the rapid rate of warming and long generation time for *L. kempii* make a shift in nesting unlikely to ultimately mitigate the effects of elevated temperatures on hatchling sex ratios and mortality. The limited thermal profile of the restricted *L. kempii* nesting range, and temperature-dependent sex determination, make this sea turtle particularly vulnerable to climate change. This vulnerability provides the opportunity to gain insights on strategies for the survival of thermally sensitive species in a warming world.

KEY WORDS: *Lepidochelys kempii* · Climate change · Temperature-sensitive sex determination · TSD · Incubation temperatures · Nesting range · Gulf of Mexico

1. INTRODUCTION

Large-scale changes in climatic patterns influence an array of taxa across diverse habitats and are driving observed changes in species phenology, behavior, and distribution (Walther et al. 2002). Ectothermic species are particularly vulnerable to the impacts of climate change, and understanding historic and current responses of thermally sensitive species to environmental changes is key for anticipating how such species will respond in the near future (i.e. within the next 100 yr), predicting extinction risk, and ensuring that effective conservation management strategies are applied (Walther et al. 2002,

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Parmesan 2006, Williams et al. 2008, Telemeco et al. 2013, Keith et al. 2014). Responses to climate change, however, often differ across taxa, encompassing phenological and physiological changes, shifts in species ranges and distributions, and changes in community and ecosystem dynamics and composition (Walther et al. 2002). Such a variety of responses can confound projections of population trends and emphasizes the need for studies evaluating species-specific responses at regional scales (Parmesan 2006, Pike 2009, Weishampel et al. 2010).

Contemporary climate change is anticipated to directly and indirectly affect various life history stages of thermally sensitive species. Sea turtles are especially vulnerable through loss of nesting habitat due to rising sea levels and intensified beach erosion, skewed sex ratios due to temperature-dependent sex determination (TSD), and increases in nest and hatchling mortality due to lethal temperatures and sand desiccation (Hawkes et al. 2007, 2009, Poloczanska et al. 2009, Fuentes & Hawkes 2011, Laloë et al. 2016, Hays et al. 2017). Sea turtles have experienced large-scale environmental changes and have responded with shifts in phenology (e.g. earlier nesting of green *Chelonia mydas* and loggerhead *Caretta caretta* sea turtles on the east coast of Florida, USA, in response to increasing sea surface temperatures; Weishampel et al. 2010), and changes in behavior and population dynamics to maintain favorable thermal conditions in habitats that span their life history (e.g. a reduction in clutch size and an increase in hatching success for loggerhead nests in response to increases in sea surface temperatures in the Mediterranean; Mazaris et al. 2008). However, such responses can vary between species (Weishampel et al. 2004, Hawkes et al. 2007, Mazaris et al. 2008, Pike 2009).

Given the rapidity of anthropogenic climate warming, whether sea turtles can adapt to abrupt large-scale ecosystem changes remains unknown (Walther et al. 2002, Parmesan 2006, Poloczanska et al. 2009, Fuentes & Hawkes 2011). The ability of sea turtles to adapt to changing environmental conditions may depend on taxon-specific variables, with species that demonstrate lower site fidelity and greater behavioral flexibility potentially reducing their extinction risk (Kamel & Mrosovsky 2005, Mrosovsky 2006, Pike & Stiner 2007). If species lack the physiological or behavioral plasticity to respond quickly enough, wildlife resource managers will be faced with identifying alternative strategies (e.g. egg hatcheries, shading nests, watering nests). Studies are especially needed for species with restricted distributions, such as the Kemp's ridley sea turtle *Lepidochelys kempii*, to better evaluate the plasticity of sea turtle responses, understand where suitable nesting habitat will occur, and protect and manage those critical habitats under predicted near-future climate change.

The Kemp's ridley sea turtle is distributed throughout the Gulf of Mexico and along the US Atlantic coast (Pritchard & Marquez 1973, Marquez 1994). The species occurs in the coastal zone within roughly 20 km from the coast, and at depths less than about 50 m (Chavez et al. 1968, Marquez 1994, Shaver et al. 2016a). Approximately 96% of Kemp's ridley nesting occurs along a 196 km stretch of beach in Tamaulipas, Mexico, and about 60% of this nesting is concentrated at a single, roughly 30 km stretch of remote beach at Rancho Nuevo, Tamaulipas. Historical documentation suggests that the geographic range of nesting in this species was once widely distributed throughout the western Gulf of Mexico, prior to its near extinction in the mid-1980s (Marquez 1994, TEWG 2000, Shaver et al. 2016a).

One hypothesized response of the Kemp's ridley to climate change-induced sea level rise could be a range shift to exploit new, suitable nesting habitats, although a variety of factors may confound this option (Hawkes et al. 2009). Unique among sea turtles, the Kemp's ridley exhibits comparatively high fidelity to a single region of beach in the western Gulf of Mexico (Pritchard & Marquez 1973, Marquez 1994, Burchfield 2014). This limited geographic distribution increases the vulnerability of this Critically Endangered species (Wibbels & Bevan 2019) and reduces its options for adapting to the impacts of climate change.

As nest incubation temperatures continue to rise, they may soon approach conditions that ultimately become unsuitable for successful hatchling production. Elevated incubation temperatures at nesting beaches can impair embryonic development at a constant incubation temperature above 33–35°C (Ackerman 1997), and when temperatures fluctuate above 35°C, hatching success is reduced in some species (Howard et al. 2014). However, these specific findings are not based on an investigation of thermal limits for all sea turtle species, and interspecific differences in thermal tolerances do exist (Howard et al. 2014). In fact, relatively high hatching success (above 77%) has been reported for *L. kempii* nests with incubation temperatures exceeding 35°C, particularly during the last third of the incubation period when metabolic heat rises, although incubation temperatures reaching 38.0–40.2°C have been associated with higher rates of embryonic mortality (Shaver et al. 1988, Shaver & Chaney 1989, Shaver & Caillouet 2015). Kemp's ridleys may have a higher lethal tem-

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perature threshold due to a shallow average nest depth, greater daily nest temperature fluctuation, and higher pivotal temperature compared to other sea turtle species (Shaver et al. 1988, Shaver & Chaney 1989, Howard et al. 2014, Caillouet et al. 2015). Thus, this specific relationship between hatching success and duration of time during incubation spent above 35°C may not apply to Kemp's ridleys.

Another key concern regarding rapid climate warming and sea turtles is that warming directly influences embryonic development through the process of temperature-dependent sex determination (TSD), whereby the sex of the embryo is determined by the incubation temperature of the nest during the middle third of the incubation period (Mrosovsky 1980, 1994, Wibbels 2003). Although many aspects of sea turtle life history are thermally sensitive (e.g. timing of reproductive activities, foraging ability, metabolism), TSD can significantly influence reproductive output, reproductive success, and ultimately, the recovery of an endangered species (Coyne 2000, Wibbels 2007). Among sea turtles, cooler nest temperatures produce more males, while warmer temperatures result in more females (Mrosovsky 1980). The range over which 100% male hatchling production shifts to 100% female is termed the transitional range of temperatures (TRT), with the temperature resulting in a 1:1 M:F sex ratio known as the pivotal temperature (Yntema & Mrosovsky 1979). For Kemp's ridleys, the TRT is approximately 29.0–32.5°C, with a 1:1 M:F sex ratio estimated to occur when the average temperature during the middle third of the incubation period is approximately 29.9–30.2°C (Shaver et al. 1988, Mrosovsky & Pieau 1991, Mrosovsky 1994, Godfrey & Mrosovsky 1999, LeBlanc et al. 2012). The TRT for sea turtles in general is rather narrow (1–3°C), suggesting that relatively minor changes in global air temperatures could significantly alter hatchling sex ratios. Climate models generated by the Intergovernmental Panel on Climate Change (IPCC) project an increase in global temperature of 0.3–4.8°C by the year 2100 (Pachauri et al. 2014). Rising global temperatures could lead to extreme female bias and male-limited populations (Wibbels 2003, Fuentes et al. 2010, Fuentes & Hawkes 2011, Braun McNeill et al. 2016, dei Marcovaldi et al. 2016, Laloë et al. 2016).

In the present study, we compared beach thermal profiles across most of the re-occupied historic nesting range of the Critically Endangered Kemp's ridley sea turtle to evaluate the availability of thermally suitable nesting habitat for this species under predicted near-future environmental conditions. The single, primary nesting location in the western Gulf of Mexico makes the Kemp's ridley a model species to evaluate the implications of near-future anthropogenic climate change on the life history and survival of an endangered species.

2. MATERIALS AND METHODS

2.1. Field protocols

Between 130 and 140 data loggers (Onset HOBO Pendant®) were buried at a depth of 35 cm each year (2014–2017) on sandy beaches every 300 m at La Pesca (LP), Tepehuajes (TEP), Rancho Nuevo (RN), Barra Del Tordo (BT), Altamira (A), and Miramar (MIR) beaches in Tamaulipas, Mexico. Data loggers were also buried at a depth of 35 cm each year (2014–2016) every 800 m at North and South Padre Island National Seashore (PAIS-N and PAIS-S, respectively) and South Padre Island (SPI), Texas, USA (Fig. 1). Relatively minimal Kemp's ridley nesting occurs on beaches at Veracruz, Mexico, to the south of those included in the present study; however, beach temperatures from Veracruz were not accessible for the current analysis. The depth of the loggers chosen coincides with the mean nest depth of Kemp's ridleys (Pritchard & Marquez 1973). Data loggers had an accuracy of ±0.3°C, and each was calibrated prior to

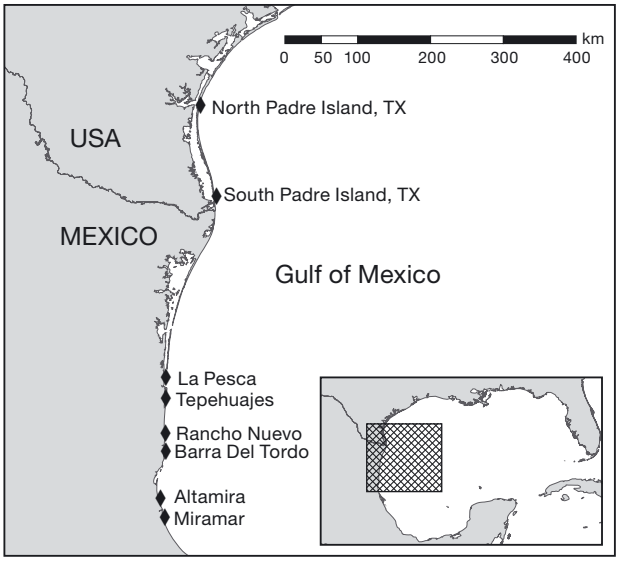

Fig. 1. Study sites across primary nesting habitat of Kemp's ridley sea turtles in the state of Tamaulipas, Mexico, as well as on Padre Island, Texas, USA. Marked locations represent beaches on which data loggers were buried to a depth of 35 cm to record sand temperatures throughout the Kemp's ridley nesting season for all locations in Mexico and Texas from 2014–2016, and for locations in Mexico only for the 2017 nesting season

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the beginning of a given nesting season in the laboratory at the University of Alabama at Birmingham (UAB) for deployment in Mexico or in the laboratory at PAIS for deployment in Texas. The timing of when a given data logger was buried in the sand varied by the beach and year of the study, but on average, data loggers were placed prior to the beginning of the annual nesting season for Kemp's ridleys (March–April). Data loggers were removed at the end of the season after all nests had emerged (August–September). Data loggers were buried along transects perpendicular to the beach at position 3, i.e. between the base of the dune and the seaward-facing slope of the primary dune, since this is the region where most nesting occurs (Marquez 1994). For comparative purposes, only data from 11 April to 20 August in each of the years (2014–2017) were analyzed, a time period that was selected to encompass the primary peak nesting and hatching season for Kemp's ridleys (Pritchard & Marquez 1973).

2.2. Data analysis

Data loggers were set to record ambient sand temperature every hour throughout the duration of the 19 wk nesting and hatching season. Following data logger recovery and transportation to UAB or PAIS, the data were downloaded to a computer. Hourly sand temperatures for each data logger were averaged to generate a daily mean (±SD) temperature. After testing the data for normality and identifying and removing statistically significant outliers from the data set, daily sand temperatures from all data loggers were analyzed using a repeated measures random effects 1-way ANOVA model with 'data logger' as a random effect in the 'nlme' package in R (Pinheiro et al. 2006). A post hoc Tukey honestly significant difference (HSD) test was used to compare daily and seasonal mean temperatures among the separate beaches and group the beaches according to similarity for each year.

3. RESULTS

Data analysis indicates that Kemp's ridley mean nesting beach temperatures during the period of nesting and hatching used in this study, hereafter called the study season (11 April–20 August), were significantly different across locations in each of the 3 years where beaches in Tamaulipas, Mexico, and Padre Island, Texas, USA, were examined (2014, 2015, 2016) (ANOVA for 2014: df = 7, $F = 42.95$, $p < 0.0001$; 2015: df = 8, $F = 131.82$, $p < 0.0001$; 2016: df = 7, $F = 107.67$, $p < 0.0001$). In 2017, only temperatures at nesting beaches in Mexico were examined, and results indicated that mean temperatures for the 4 study seasons were significantly different from each other (ANOVA, df = 5, $F = 10.5$, $p < 0.0001$; Fig. 2). Additionally, mean

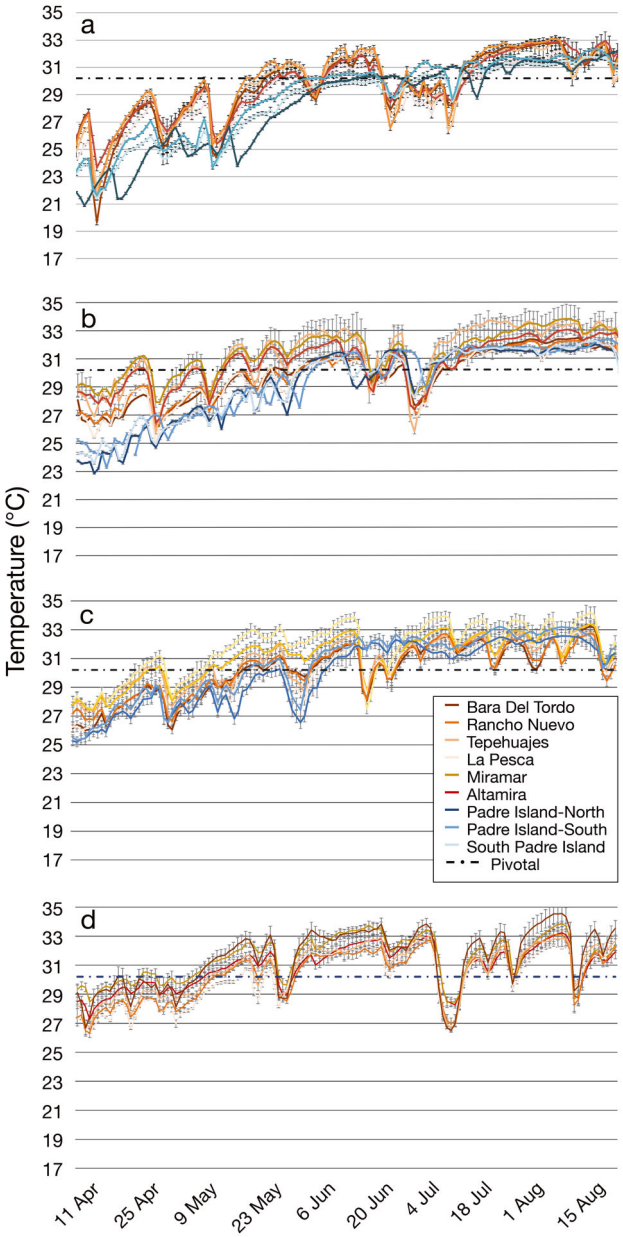

Fig. 2. Mean (±SD) daily sand temperatures recorded at study locations throughout the nesting range of Kemp's ridley sea turtles in Tamaulipas, Mexico, and Padre Island, Texas, USA, during (a) 2014, (b) 2015, and (c) 2016. (d) Mean daily beach temperatures recorded only at study locations in Mexico during the 2017 study season. The dashed-dotted line represents the pivotal temperature that results in an approximate 1:1 fe male:male hatchling sex ratio in *Lepidochelys kempii*

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beach temperatures at each location were significantly different across all years included in this study (ANOVAs for each location = 0). A and MIR beaches are among the warmest locations we examined given the strong inverse correlation between latitude and rising environmental temperatures (Rind 1998, Hays et al. 2001). Mean nesting beach temperatures at LP (monitored from 2014–2017) and PAIS (monitored from 2014–2016) provide additional support for this pattern and were consistently the lowest of the beaches monitored in the current study. There was no consistent latitudinal pattern in temperature for the beaches at RN, TEP, and BT with respect to the other beaches in Mexico.

Table 1. Tukey HSD comparisons of mean (±SD) beach temperatures (°C) recorded from 11 April to 20 August from 2014–2016 at study sites throughout the nesting range of Kemp's ridley sea turtles *Lepidochelys kempii* in Tamaulipas, Mexico, and Padre Island, Texas, USA. Values during the 2017 nesting season represent temperatures recorded only at study sites in Mexico. PAIS-N (PAIS-S): northern (southern) Padre Island National Seashore; SPI: South Padre Island; LP: La Pesca; BT: Barra Del Tordo; TEP: Tepehuajes; A: Altamira; RN: Rancho Nuevo. Means sharing the same superscript letter are not statistically different ($p > 0.05$) in Tukey's HSD pairwise tests

Year	Beach	Mean temperature
2014	PAIS-N	27.4 (±3.9)[a]
	PAIS-S	28.1 (±3.5)[ab]
	SPI	27.6 (±3.4)[a]
	LP	28.4 (±2.8)[abc]
	TEP	29.0 (±2.8)[bc]
	RN	29.3 (±2.9)[c]
	BT	29.0 (±3.0)[bc]
	A	29.1 (±2.7)[bc]
2015	PAIS-N	29.3 (±2.7)[a]
	PAIS-S	29.5 (±2.5)[a]
	SPI	29.4 (±2.5)[a]
	LP	29.8 (±1.8)[a]
	TEP	31.3 (±2.0)[c]
	RN	30.0 (±1.8)[a]
	BT	30.0 (±1.8)[a]
	A	30.8 (±1.7)[c]
	MIR	31.5 (±1.6)[c]
2016	PAIS-N	29.8 (±2.4)[a]
	PAIS-S	30.4 (±2.4)[ab]
	LP	30.0 (±2.1)[ab]
	TEP	30.7 (±1.8)[b]
	RN	30.1 (±2.0)[ab]
	BT	30.0 (±2.2)[ab]
	A	31.0 (±1.8)[bc]
	MIR	31.6 (±2.0)[c]
2017	LP	30.2 (±1.9)[a]
	TEP	30.7 (±1.8)[b]
	RN	30.4 (±2.0)[a]
	BT	31.5 (±2.1)[c]
	A	30.9 (±1.7)[b]
	MIR	31.5 (±1.7)[c]

Comparing the mean nesting beach temperatures recorded during the nesting season from 2014–2016 at study sites in Texas and Mexico, the largest difference between the highest and lowest mean beach temperature was recorded during the 2015 nesting season at 2.2°C between PAIS-N and MIR (Table 1 and Table A1 in the Appendix). Comparing mean beach temperatures recorded at study sites only in Mexico across all 4 years of the study, the greatest difference between the maximum and minimum mean beach temperature was 1.7°C between LP and MIR during the 2015 nesting season (Table A1). The highest mean beach temperature for a nesting season observed during this study was 31.6 ± 2.0°C recorded at MIR in 2016 (Table 1). Post hoc Tukey HSD comparisons of mean beach temperatures at study locations in Texas and Mexico during the 2014–2016 nesting seasons and at study locations only in Mexico during the 2017 nesting season grouped mean beach temperatures into 2–3 temperature subsets depending on the year (Table 1).

Collectively, the results from the current study show that mean nesting beach temperatures throughout Mexico and Texas were statistically different from each other throughout the 2014–2016 nesting seasons, with mean beach temperatures generally decreasing with increasing latitude. Similarly, mean nesting beach temperatures at study sites in Mexico were statistically different from each other in the 2017 nesting season and generally warmer than northern beaches in Texas. In all 4 study years (2014–2017), MIR beach in Mexico was consistently grouped among the nesting beaches with the highest mean beach temperatures, while LP beach in Mexico and PAIS-N in Texas were consistently grouped among the nesting beaches with the lowest temperature in each year.

4. DISCUSSION

The present study indicates that a relatively restricted range of beach temperatures occurs over the nesting season throughout the nesting range of Kemp's ridley sea turtles. Despite this, critical biological events, such as the determination of hatchling sex, occur within this limited thermal window (Wibbels 2003). This narrow range of temperatures in which important biological events occur could be disadvantageous to the ultimate survival of Kemp's ridleys considering that conservative IPCC climate models project increases in environmental temperatures of approximately 1°C by 2100 (Pachauri et al.

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2014). Although increases in surface temperatures will not cause equivalent and simultaneous increases in sand incubation temperatures at nest depth, even minor (~1°C) increases in incubation temperatures can skew hatchling sex ratios (Janzen 1994, Hawkes et al. 2007) and adversely impact the timing and success of hatchlings (Fuentes & Hawkes 2011). Further, temperature changes could alter the timing of migration and onset of nesting in adults (Weishampel et al. 2004, 2010) and disrupt the timing of linkages between the movements of temperature-sensitive species and the availability of critical resources such as prey (Walther et al. 2002, Parmesan 2006, Schwanz & Janzen 2008). Our study demonstrates that the Kemp's ridley provides an opportunity to evaluate the impacts of anthropogenic climate change on a thermally sensitive species and emphasizes that for some species, opportunities to adapt to long-term environmental changes may be limited.

Our findings suggest that northern beaches in Texas and Mexico, such as LP, SPI, and PAIS, could provide cooler incubation temperatures and suitable nesting habitat under a predicted near-future climate warming scenario than beaches to the south, where the majority of Kemp's ridley nesting currently occurs. Therefore, these northern beaches should receive priority when considering the conservation of this species. It is important to note that the results in the present study document the average sand temperatures at mean nest depth (35 cm) for these beaches during the study season. Mean nesting beach temperatures observed for the study season at the northern end of PAIS and LP fell below the temperature producing a 1:1 M:F sex ratio (approximately 30°C; Wibbels 2003). However, actual nest temperatures would be higher due to embryo metabolic heating. Further, depending on the lay date, nest depth, beach vegetation, sand characteristics, and amount of rainfall, nests experience temperatures that are cooler or warmer than the overall mean for a given location (Liles et al. 2019). Also, the position of an egg within the nest can influence the incubation temperatures experienced by each egg. Eggs deeper in the nest experience cooler temperatures than those located nearer the top of the nest, and eggs positioned toward the center of the nest are more influenced by metabolic heating relative to those located near the periphery (Godfrey et al. 1997, Broderick et al. 2001). Thus, it is possible that eggs located near the periphery or deeper within the nest may incubate at male-producing temperatures, while eggs towards the center of the nest incubate at female-producing temperatures. Regardless, applying a conservative climate warming scenario of an increase in beach temperatures of 1–2°C by the year 2100 (Pachauri et al. 2014), beach temperatures could increase to at least an estimated mean of 30°C at PAIS, as an example. Under this scenario, temperatures on cooler beaches (LP, SPI, and PAIS) would still favor the production of mixed hatchling sex ratios, with at least some production of male hatchlings for the species.

Despite the potential of northern beaches to offer respite under a near-future climate change scenario, the lengthy age to maturity (approximately 11 yr; Caillouet et al. 2011), conserved mechanisms of sex determination, and fidelity of this species to southern nesting beaches diminish the likelihood that a natural shift in nesting distribution will occur rapidly enough to compensate for the impacts of climate change (Poloczanska et al. 2009). The majority of female Kemp's ridleys currently nest on southern beaches (only approximately 10% of annual nesting currently occurs on northern beaches in Texas and Mexico; J. J. Peña pers. obs.) that could become unsuitable nesting habitat in the future. Under a conservative climate warming scenario, beach temperatures in Mexico throughout the southern portion of the Kemp's ridley nesting range will reach temperatures that could yield extreme female bias, if not 100% female hatchling cohorts, and reduced hatching success due to lethal temperatures and sand desiccation.

Although the increase in female hatchlings under a conservative climate warming scenario could initially result in greater reproductive output and population growth, a decreasing proportion of male turtles in the population could eventually lead to fewer mating opportunities for Kemp's ridleys (Coyne 2000, Jensen et al. 2018). However, lethal incubation temperatures could present a more immediate risk to species survival than extreme female bias (Hays et al. 2017). As an example, mean sand temperatures at 35 cm depth could increase to a high of approximately 34°C at MIR beach in Mexico. These sand temperatures would approach the reported upper thermal limit for embryonic development in some species, such as green and loggerhead sea turtles (above approximately 33–35°C, reviewed by Howard et al. 2014), potentially leading to increased mortality (Fuentes & Porter 2013). Additionally, these projections do not account for metabolic heating that would further elevate temperatures within nests. Although the impacts of such higher temperatures on Kemp's ridley nests have not been evaluated (Howard et al. 2014), it is possible that Kemp's ridleys may be more tolerant to the higher projected sand incubation temperatures, which could help to mitigate the consequences of a

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warming environment. Preference for the southern beaches in the Kemp's ridley nesting range is maintained through the successful production of hatchlings that return to these beaches after they reach sexual maturity (Heppell et al. 2003, Hawkes et al. 2009). A decline in hatching success on southern beaches due to lethal incubation temperatures over many generations could gradually shift the epicenter of nesting north to beaches where hatching success may remain relatively high (Hawkes et al. 2009). However, such a gradual shift in the primary nesting location may occur at a slower rate than that of increasing environmental temperatures and thus limit the potential of this strategy to mitigate the adverse consequences of climate change.

Other potential adaptations to changing environmental temperatures have been hypothesized for Kemp's ridleys, including altered nesting behavior (i.e. selecting nest sites that maintain a favorable thermal incubation environment), changes in nesting phenology, or shifts in the parameters of sex determination (i.e. altered pivotal temperature and TRT; Hulin & Guillon 2007). Additionally, these responses may be regulated by environmental temperature changes at non-reproductive habitats. Sea surface temperatures influence nesting chronology (Pike 2009, Weishampel et al. 2010), the timing of migration to breeding grounds (Hawkes et al. 2007, Mazaris et al. 2008), and measures of fecundity (Lamont & Fujisaki 2014) in sea turtles. As an example, cooler ocean temperatures in Kemp's ridley foraging habitat in the northern Gulf of Mexico during the 2009–2010 winter were associated with a delay in nesting for the 2010 season (Gallaway et al. 2016). Thus, it is likely that sea surface temperatures in the Gulf of Mexico influence nesting trends for Kemp's ridleys. However, the physiological mechanisms of sea turtle sex determination are relatively conserved across populations, and the capacity of these long-lived species to respond rapidly to environmental selection pressure is questionable (Avise et al. 1992, Hulin & Guillon 2007, Hawkes et al. 2009, Liles et al. 2019). Based on Kemp's ridley nesting trends on the Texas coast, there is no indication of an earlier shift in the peak of nesting toward cooler months of the year (Shaver et al. 2016b), and how reproductive behavior and nesting phenology of Kemp's ridleys are regulated by ocean temperatures needs further research (Shaver et al. 2016b). Considering that the rate of average sea surface temperature warming for the Gulf of Mexico is projected to be 0.37°C per decade by the end of the century (Alexander et al. 2018), ocean temperatures should be considered when evaluating trends in Kemp's ridley nesting phenology in response to climate change.

The IPCC has generated climate models that project increases in global mean surface temperature of 2.6–4.8°C by the year 2100 (Pachauri et al. 2014). Short-term extremes in surface/air temperature would not directly and immediately translate to a change in sand temperature at nest depth of the same magnitude, as thermal energy attenuates in the sand, which can dampen temporary extremes (Hays et al. 2001). However, long-term, sustained changes in mean air temperature would be expected to result in equivalent changes in mean sand temperature. To provide insight into the impacts of a long-term increase in sand incubation temperatures, we evaluated the results from the present study in the context of a hypothetical increase in sand temperatures of approximately 4°C. An end-of-century increase in sand temperatures of up to 4°C could increase mean nesting beach temperatures on north PAIS to an estimated 31°C, which would result in nearly all female hatchlings, given current physiological constraints of sex determination. It is possible that despite statistically different mean sand temperatures between Mexico and Texas beaches, these differences are not great enough under an extreme warming scenario to ultimately compensate for the impacts of rising sand and environmental temperatures associated with a warming climate and could render the northern beaches in our study (e.g. PAIS and LP) no longer capable of supporting the critical production of at least some male hatchlings for the species.

Conservation strategies to address rapid anthropogenic environmental warming throughout the nesting range of Kemp's ridleys include identifying and protecting future critical nesting habitat, as well as human intervention to manipulate nest incubation conditions (Jourdan & Fuentes 2015). Strategies involving human intervention range from relocating nests from suboptimal beaches to hatcheries or artificial incubators such as polystyrene boxes, shading, sprinkling with water or using shade from native vegetation to cool the sand incubation temperatures of *in situ* nests (Kamel & Mrosovsky 2006, Fuentes et al. 2012). Although some of these procedures have been used successfully for decades and continue to be used to protect Kemp's ridley eggs (Shaver & Caillouet 2015), the effectiveness of these approaches to mitigating the impacts of increasing sand temperatures on nest incubation conditions has not been adequately quantified (Jourdan & Fuentes 2015). Nest management strategies currently used in Tamaulipas, Mexico, call for relocating as many Kemp's ridley

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nests as possible to nearby hatcheries throughout the nesting season and moderating nest incubation conditions by using mesh shading across the top of the hatchery and sprinkling the sand with water (J. J. Peña pers. obs.). Nests laid at PAIS are relocated to either egg hatcheries or facilities that allow optimal incubation conditions to be closely monitored and maintained (LeBlanc et al. 2012). Since maintaining optimal hatchling sex ratios and high hatching success at primary nesting beaches in Mexico and Texas currently necessitates the use of these protocols, it is possible that the efficacy of these methods alone may be diminished given the higher sand temperatures anticipated by the end of the century.

Considering alternative future strategies, annually relocating more than approximately 24 000 Kemp's ridley nests (24 591 total registered Kemp's ridley nests in the 2017 season, J. J. Peña pers. obs.) from warmer beaches in the nesting range to relatively cooler beaches may not be financially or logistically feasible or sustainable through the end of the century (Fuentes & Hawkes 2011). However, it is possible that a subset of nests could be relocated from beaches in Mexico to artificial incubation facilities or reburied on thermally suitable beaches at the northern extent of the Kemp's ridley nesting range. Incubation facilities, such as those currently used at PAIS, can reliably result in hatching success rates that are comparable to and higher than those of *in situ* nests (Shaver & Wibbels 2007, Shaver & Caillouet 2015) with care to protect nests from movement-induced mortality (Eckert & Eckert 1990). Relocating a portion of Kemp's ridley nests from primary beaches in Mexico to incubation facilities or alternative nesting beaches in Texas represents a reliable protocol that, if necessary, could be integrated into the larger context of mitigating the impacts of a warming nesting range for this species (Shaver & Caillouet 2015).

In summary, the ranges of collective temperatures experienced at beaches throughout the nesting distribution of Kemp's ridley sea turtles are significantly different from each other, with some beaches at the northernmost extent of this range providing incubation temperatures that could initially mitigate increasing environmental temperatures under conservative end-of-century climate warming scenarios. However, due to behavioral, physiological, and evolutionary constraints, it is unlikely that Kemp's ridleys will have the capacity to naturally respond to these changes given the rapid rate of projected environmental temperature change. Thus, this study provides insight on beaches that could proximally offer suitable habitat to produce a mixed sex ratio of hatchlings and may be used as an integral part in strategies to artificially mitigate the impacts of climate change on this species. Yet, the differences in mean beach temperatures across the nesting range may not be sufficient to support a mixed hatchling sex ratio for Kemp's ridleys under extreme climate change scenarios. Considering that nearly the entire population of this species nests in a relatively limited geographic range, the Kemp's ridley represents a species with limited options for adapting to climate change. As such, the Kemp's ridley is a sentinel species by which to evaluate the impacts of near-future, anthropogenic climate change on the survival of a thermally sensitive species of sea turtle.

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APPENDIX

Table A1. Minimum and maximum nesting season mean ± SD beach temperatures (°C) recorded at study sites across the nesting range of Kemp's ridley sea turtles *Lepidochelys kempii* in 2014–2016 at locations in the State of Tamaulipas, Mexico, and Padre Island, Texas, USA. In 2017, only locations in Mexico were investigated. PAIS-N: northern Padre Island National Seashore; RN: Rancho Nuevo; MIR: Miramar; LP: La Pesca; BT: Barra Del Tordo

Year	Min temp (Location)	Max temp (Location)	Difference (°C)
2014	27.4 ± 3.9 (PAIS-N)	29.3 ± 2.9 (RN)	1.9
2015	29.3 ± 2.7 (PAIS-N)	31.5 ± 1.6 (MIR)	2.2
2016	29.8 ± 2.4 (PAIS-N)	31.6 ± 2.0 (MIR)	1.7
2017	30.2 ± 1.9 (LP)	31.6 ± 2.1 (BT)	1.3

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