



Impacts of nest temperatures on leatherback reproductive success, hatchling morphology, and performance in South Florida

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ABSTRACT: Leatherback turtles *Dermochelys coriacea* are experiencing population declines due to various anthropogenic threats. Beaches play a crucial role in the survival of sea turtle species since reproductive success is affected by environmental conditions inside the nest. Climate change is predicted to increase sand temperatures and affect rainfall, which will change the nest microenvironment, and thus may alter not only hatch and emergence success but also hatchling morphology and performance. This study examined the relationship between nest incubation temperatures and leatherback hatchling terrestrial performance, as the crawl from the nest to the sea is a critical phase for hatchling survival. Temperature data loggers were placed in 12 leatherback turtle nests on the day they were laid across the early, middle, and late South Florida nesting season. Upon emergence, hatchlings were tested for righting ability and crawling speeds. Mean nest temperatures ranged from 29.0 to 32.5°C and were significantly higher in mid- and late-season nests compared to early-season nests. Hatching and emergence success correlated with temperature, where the mid-season nests were the most successful. Hatchling morphology also correlated with temperature; nests with lower temperatures produced larger hatchlings than nests with hotter temperatures. Righting response scores were significantly lower in hatchlings from late-season, hotter nests, while there was no correlation between crawling speeds and temperature. However, more studies are needed to investigate these relationships since the sample size of this study was relatively small. Our data provide insight into how rising nest temperatures may impact hatchling performance and, in turn, affect their survival.

KEY WORDS: Leatherback · Morphology · Performance · Climate change

1. INTRODUCTION

Beaches are critically important for sea turtle species. Leatherback turtles *Dermochelys coriacea* nest on tropical and subtropical beaches worldwide and are listed on the IUCN Red List as Vulnerable (Northwest Atlantic Leatherback Working Group 2018). Southeastern Florida beaches have some of the highest leatherback nesting numbers in the USA, but as with sea turtle populations globally, direct anthropogenic factors and climate change may threaten their persistence. Climate change has been increas-

ing atmospheric temperatures, which may rise 1 to 5°C above the current temperatures by the year 2100 (IPCC 2014). The expected increase is concerning for conservation efforts (Hamann et al. 2013), since rapid environmental changes can make it harder for organisms to adapt to the changed climatic conditions. A rise in temperature will have the most significant impact on organisms whose physiology is dependent upon environmental temperatures (Deutsch et al. 2008). Sea turtles are susceptible to a significantly warmer environment since their eggs incubate in the sand without parental care, and

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developmental success is thus dependent on sand characteristics including incubation temperatures (Bolten et al. 2011).

Incubation temperatures are not only impacted by sand temperatures; nest temperatures are also increased by metabolic heat produced by the developing embryos themselves, mostly towards the end of the incubation period (Zbinden et al. 2006). Increasing sand temperatures due to climate change coupled with metabolic heating from the developing embryos can lead to average nest temperatures above 34°C in some areas and during certain portions of the nesting season; 34°C is thought to be the approximate upper critical temperature for sea turtles during early embryonic development (Ackerman 1997), but more recent studies have shown later-stage embryos can tolerate multiple days at temperatures of 34 to 36°C (Broderick et al. 2001, Carthy et al. 2003, Maulany et al. 2012b, Booth et al. 2013). When nests rise above this critical maximum, there is often an associated decrease in hatching success and hatchling performance, depending on the developmental stage (Maloney et al. 1990, Matsuzawa et al. 2002, Bladow & Milton 2019). Embryo mortality has been shown to increase with increasing temperatures, which can lead to a decrease in hatch and/or emergence success (Matsuzawa et al. 2002, Garrett et al. 2010, Kobayashi et al. 2017, Booth & Dunstan 2018, Bladow & Milton 2019). There is also an association between elevated incubation temperatures and an increase in the frequency of developmental abnormalities (Telemeco et al. 2013, Zimm et al. 2017, Ingle et al. 2021, Tanabe et al. 2021), as well as a link between hotter nest temperatures and poorer hatchling performance (Ischer et al. 2009, Sim et al. 2014, Wood et al. 2014), including in leatherbacks (Rivas et al. 2019).

Incubation temperatures also impact the incubation period of sea turtle eggs, where the length of incubation increases at cooler temperatures and decreases at warmer temperatures (Hendrickson 1958, Kaska et al. 1998), resulting in altered embryonic growth rates (Hendrickson 1958, Miller 1985). Hatchlings coming from nests incubated at higher temperatures are often smaller in size, with a larger yolk reserve, while the reverse is true for hatchlings coming from nests incubated at lower temperatures (Booth 2017, Rivas et al. 2019). A larger body size could mean hatchlings can better escape predators by crawling or swimming faster, as well as reduce the chance of being preyed upon by gape-limited predators (Booth et al. 2004, Salmon et al. 2015), though a larger yolk reserve could be beneficial when search-

ing for food and as an energy source in the initial swim offshore (Booth et al. 2004). Conversely, a large yolk reserve and less muscle tissue in smaller hatchlings could potentially hinder the hatchling's performance, which in turn would decrease their survival if they are unable to make it to the water (Booth et al. 2004). Previous studies on loggerhead turtles *Caretta caretta* and green turtles *Chelonia mydas* have found increased incubation temperatures resulted in a decrease in locomotion performance in the water and on land (Ischer et al. 2009, Fisher et al. 2014, Henaghan 2018, Fleming et al. 2020), while leatherback nest relocation to a shaded area resulted in larger hatchlings with better crawling and righting abilities than those from nests exposed to the sun (Rivas et al. 2019). Since the crawl from the nest to the water is a time of potentially high predation (Santidrián Tomillo et al. 2010, Erb & Wyneken 2019), poorer physical performance could increase mortality. We are still investigating why temperature influences performance, however; one possible explanation is morphological differences in the carapace and flippers due to differential growth rates during incubation (Booth et al. 2004, Mickelson & Downie 2010, Fisher et al. 2014, Fleming et al. 2020).

Leatherback turtle hatchling flippers are larger than those of most other species of sea turtles, and their crawling gait is characterized as a rowing movement, where the front flippers have synchronized movement on each side to move the body forward (Davenport 1987, Wyneken 1997). It has been suggested that this gait is more advantageous to leatherback hatchlings with narrow bodies and longer flippers compared to hatchlings with shorter flippers and wider bodies (Mickelson & Downie 2010). Studies on nest temperatures and hatchling performance to date have focused primarily on green (e.g. Ischer et al. 2009, Henaghan 2018) and loggerhead (e.g. Fisher et al. 2014, Henaghan 2018, Fleming et al. 2020) sea turtles. There have been a few studies on leatherback turtle nest temperatures and hatchling performance, but no study has been conducted in the USA (Mickelson & Downie 2010, Rivas et al. 2019, Bandimere et al. 2021). Leatherback turtle nests have low hatching success compared to other sea turtle species (Bell et al. 2004, Rafferty et al. 2011, Perrault et al. 2012), and increased temperatures hinder the performance of leatherback hatchlings upon emergence, suggesting the species could be more vulnerable to population declines resulting from climate change. The present study aimed to build on earlier work on green and loggerhead turtles in South Florida and leatherback turtles in other

parts of the world, by examining leatherback turtle nests in South Florida, to determine how incubation temperatures may affect hatching success, emergence success, hatchling morphology, and locomotor performance (crawling and self-righting response). Since leatherback nests, on average, are deeper than those of other species (Standora & Spotila 1985, Miller 1997, Booth & Astill 2001, Wallace et al. 2007, Santidrián Tomillo et al. 2017) and are typically laid in cooler months (Florida Fish and Wildlife Conservation Commission 2016), we hypothesized that they would have lower nest temperatures than those reported in other sea turtle species on South Florida beaches. We hypothesized that, as in other species and as in leatherback sea turtles in other locations, higher nest temperatures would result in lower hatching and emergence success and also result in lower hatchling locomotor performance.

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted on 9.6 km of beach in Juno Beach, Florida, USA. Juno Beach is located in northeastern Palm Beach County and was selected for this study due to the relatively high density of leatherback (*Dermochelys coriacea*) nests found at this location (Stewart et al. 2014). Leatherback turtles in this region generally begin nesting in February and are largely done by June; nests used in this study (12 in total and 115 hatchlings) were laid between 27 March and 14 June 2019.

2.2. Nest temperature

For this study, we divided the nesting season into early nests (4 nests laid between 27 Mar and 18 Apr), a mid-season group (4 nests laid between 3 and 16 May), and a late-season group (5 nests laid between 20 May and 14 Jun), based on the seasonal patterns of nesting in previous years. Either immediately following egg deposition or the morning after, a sea turtle specialist from the Loggerhead Marinelifelife Center carefully removed the top egg layers and placed an Onset HOBO-U22 thermologger (accuracy of $\pm 0.2^{\circ}\text{C}$; Onset Computer) at the approximate center of each clutch before replacing the eggs. The thermologgers recorded temperature throughout the incubation period at 30 min intervals. An average of the 30 min intervals was calculated to obtain the daily mean

temperature of each nest. The highest mean 3 d temperature was also calculated by generating rolling averages of the temperature intervals. The overall mean incubation temperature and the maximum temperature for each nest were also identified.

2.3. Hatchling collection

When emergence was expected, permanent restraining cages were placed over the nests and checked periodically throughout the night(s). Upon emergence, an average of 10 (range 7–10, mean 9.7) hatchlings were collected per nest and placed in a dark cooler with warm damp sand for transport to laboratory facilities at the Loggerhead Marinelifelife Center in Juno Beach.

2.4. Body morphology and body condition index

To evaluate hatchling morphology, digital calipers were used to measure standard straight carapace length (SCL, cm), straight carapace width (SCW, cm), body depth (BD, cm), and flipper length (cm). Right and left flipper lengths were averaged to calculate the average flipper length for each individual hatchling. Mass (g) was determined using a digital scale. Body condition index (BCI) was evaluated using the formula adapted from Bjorndal et al. (2000):

$$\text{BCI} = (\text{mass} / \text{SCL}^3) \times 10\,000$$

2.5. Hatchling locomotor performance

Hatchlings were placed one at a time on their carapace in a 5 gallon (19 l) bucket filled halfway with sand. The time it took for the hatchling to right itself onto its plastron was recorded. Each individual righting trial lasted for a maximum of 30 s; the test ended when the hatchling had self-righted 3 times or the trial had been repeated 6 times, whichever came first. Between each trial, the hatchling had a rest period of 10 s. The hatchlings received a propensity score (adapted from Booth et al. 2013) from 0 to 6, with 0 meaning failure to self-right in any of the 6 trials and 6 indicating successfully self-righting 3 times in a row (Table 1). The mean righting response was calculated for each group. After completing the righting response trials, the hatchlings were placed in a sand-covered arena approximately 1 m in diameter. A light was placed at one side of the arena to give a directional cue, and the hatchlings were re-

Table 1. Hatchling self-righting propensity scores and definitions. Adapted from Booth et al. (2013)

Score	Condition
0	No righting event in 6 trials
1	1 righting in 6 trials
2	2 rightings in 6 trials
3	3 rightings in 6 trials
4	3 rightings in 5 trials
5	3 rightings in 4 trials
6	3 rightings in 3 trials

leased one at a time on the side opposite the light. The time it took them to crawl ~1 m was recorded. The distance they crawled was measured with a meter tape measure and used to calculate crawling speed.

2.6. Hatching and emergence success

Nests were excavated 3 d after the initial mass emergence based on recommendations from the Florida Fish and Wildlife Conservation Commission (2016). During the excavations, hatching success, emergence success, and the top and bottom depths of the egg chamber were recorded. Hatching success was calculated by dividing the number of hatched eggshells by the total clutch size. Emergence success was calculated by subtracting the number of hatchlings found in the nest by the number of hatched eggshells and dividing it by the total clutch size (Miller et al. 1999).

2.7. Statistical analysis

The data were analyzed for statistical significance using the RStudio 2023.031+446 (R Core Team 2012). The data were first tested for normality using the Shapiro-Wilk test, and it was found that all of the data violated the assumptions of normality. A Kruskal-Wallis rank sum test was performed on the data for temperature, incubation period, hatching success, emergence success, body measurements, propensity score, and crawling speed between the 3 groups (early-, mid-, and late-season nests). If the results were significant, a comparison using a pairwise post hoc Dunn's test with Bonferroni adjustments (for temperature data) and a pairwise Wilcoxon rank sum test was conducted to see which groups were significantly different from each other. Since the sample size for each group was small, exact critical

values from Conover (1999) were used to confirm the significance between groups. Spearman's rank correlations were used to determine associations between temperature, incubation period, hatching success, emergence success, body measurements, propensity score, and crawling speed. A polynomial least-squares regression was performed on hatching success and mean nest temperatures, as well as on emergence success and mean nest temperatures, to show the relationship between nest success and mean nest temperature.

3. RESULTS

3.1. Seasonal nest temperatures

Mean (\pm SD) temperatures for individual nests ranged from 29.0 ± 3.4 to $32.5 \pm 1.5^\circ\text{C}$ across the season and increased as incubation progressed (Fig. 1). The mean nest temperatures differed significantly ($\chi^2(2) = 105.53$, $p \leq 0.0001$; early vs. late: $p \leq 0.0001$; early vs. mid: $p \leq 0.0001$; mid vs. late: $p \leq 0.0001$) between the early-, mid-, and late-season nests, with median incubation temperatures of 29.3, 31.1, and 32.0°C , respectively (Table 2). For the maximum incubation temperatures ($\chi^2(2) = 28.59$, $p \leq 0.0001$; early vs. late: $p \leq 0.0001$; early vs. mid: $p \leq 0.0001$; mid vs. late: $p = 0.25$), early-season nests were significantly different from mid- and late-season nests, though mid- and late-season nests were not significantly different from each other (Table 2). The nest having the highest (maximum half-hour interval) incubation temperature was a nest laid during the mid-season (11 May) that reached 36.4°C during the

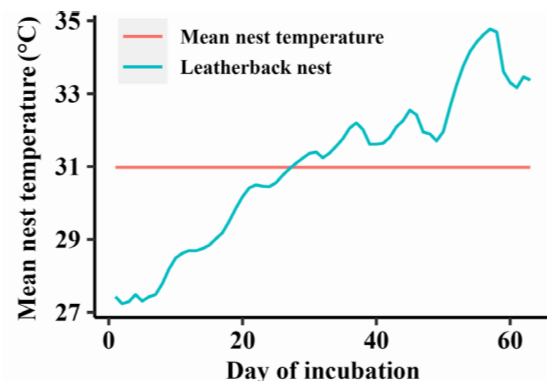


Fig. 1. Representative daily mean temperature profile of a leatherback turtle (*Dermodochelys coriacea*) nest. The nest had an overall mean temperature of 31.0°C and a maximum temperature of 35.0°C . The leatherback nest was a mid-season nest laid 5 May and had an incubation period of 62 d

Table 2. Median (ranges in parentheses) leatherback turtle (*Dermochelys coriacea*) nest incubation temperatures and period of individual nests on Juno Beach, Florida, USA. Data with different letters are significantly different from each other for the same category ($p \leq 0.05$). $n = 4$ nests for each part of the nesting season (early, mid, and late). Maximum temperature was recorded in the last week of incubation for all groups

	Time of season		
	Early 27 Mar–18 Apr	Mid 3–16 May	Late 20 May–14 Jun
Nest incubation temperature (°C)	29.3 ^a (29.0–30.1)	31.1 ^b (30.7–31.0)	32.0 ^c (32.0–32.5)
Maximum temperature (°C)	33.6 ^a (33.2–35.2)	34.7 ^b (34.4–35.6)	35.1 ^b (34.8–35.4)
Mean 3 d maximum temperature (°C)	33.6 ^a (33.1–34.8)	34.5 ^b (34.2–35.6)	34.7 ^b (34.7–35.0)
Incubation period (d)	67 ^a (64–76)	61 ^b (60–62)	58 ^c (58–60)

Table 3. Summary of leatherback turtle (*Dermochelys coriacea*) nest success and significant correlations with nest temperatures. Numbers are reported as medians. Data with different letters indicate significant differences between groups in the same category ($p \leq 0.05$). $n = 4$ nests for each part of the nesting season

	Time of season		
	Early 27 Mar–18 Apr (29.0–30.1°C)	Mid 3–16 May (30.7–31.0°C)	Late 20 May–14 Jun (32.0–32.5°C)
Hatching success (%)	44.2 ^a	69.3 ^b	49.2 ^a
Emergence success (%)	37.2 ^a	50.5 ^b	34.4 ^a
Incubation period (d)	67 ^a	61 ^b	58 ^c

last week of incubation. This nest also had the highest mean 3 d maximum incubation temperature, with an average of $35.6 \pm 0.7^\circ\text{C}$ over a single 3 d period in the last week of incubation. For the mean 3 d maximum temperatures overall ($\chi^2(2) = 29.05$, $p \leq 0.0001$; early vs. late: $p \leq 0.0001$; early vs. mid: $p \leq 0.0001$; mid vs. late: $p = 0.07$), only the early-season nests differed significantly from the mid- and late-season nests (Table 2).

3.2. Overall nest success and temperature

There was a negative correlation between nest temperature and the incubation periods of nests (mean $p \leq 0.0001$, corr. = -0.949 ; maximum $p \leq 0.001$, corr. = -0.283 ; 3 d mean $p \leq 0.003$, corr. = -0.269). The coolest nest (laid 27 May), with a mean (\pm SD) incubation temperature of $29.0 \pm 3.4^\circ\text{C}$, had the longest incubation period at 76 d. The hottest nest (laid 5 Jun), with a mean incubation temperature

of $32.5 \pm 1.6^\circ\text{C}$, had the shortest incubation period at 58 d.

Hatching success of the nests ranged from 12 to 80%, while emergence success ranged from 10 to 77%. Hatching success varied with nest temperature; hatching success increased as mean nest temperatures increased up to $\sim 31.0^\circ\text{C}$ but then decreased with temperatures above $\sim 31.5^\circ\text{C}$ (Table 3, Fig. 2). The mid-season nests had the highest median hatching ($\chi^2(2) = 45.61$, $p \leq 0.0001$; early vs. late: $p = 0.06$; early vs. mid: $p \leq 0.0001$; mid vs. late: $p \leq 0.0001$) and emergence success ($\chi^2(2) = 23.19$, $p \leq 0.0001$; early vs. late: $p = 0.07$; early vs. mid: $p \leq 0.01$; mid vs. late: $p \leq 0.0001$), and the early-season nests had the lowest median hatching and emergence success (Table 4). The size of the hatchlings also statistically correlated with hatching and emergence success (Table 4).

3.3. Overall hatchling morphology

The size of the hatchlings was influenced by temperature. Nests with lower temperatures produced longer hatchlings (maximum $p = 0.002$, corr. = -0.291 ; 3 d mean $p = 0.002$, corr. = -0.287), and nests

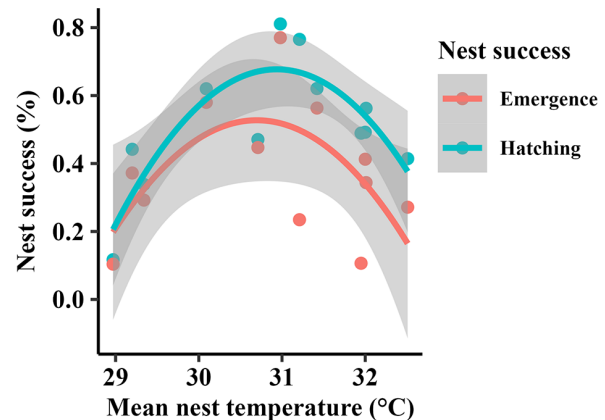


Fig. 2. Effects of mean nest temperature on hatching and emergence success of leatherback turtle (*Dermochelys coriacea*) nests ($n = 12$). Hatching and emergence showed a similar pattern, where nests incubating at either lower or hotter temperatures had low nest success. A polynomial linear regression line was fitted to both hatching and mean nest temperatures ($y = -0.1217x^2 + 7.5327x - 115.85$, $R^2 = 0.729$) and emergence success and mean nest temperatures ($y = -0.1104x^2 + 6.7803x - 103.54$, $R^2 = 0.4029$). Gray shading around each line indicates 95% CI

Table 4. Correlations between different measures of hatchling morphology and leatherback turtle (*Dermochelys coriacea*) hatching and emergence success (n = 115 hatchlings)

Variable	p	Correlation
Straight carapace width (mm) and hatching success (%)	<0.02	0.215
Straight carapace length (mm) and hatching success (%)	<0.0001	0.402
Mass (g) and hatching success (%)	<0.0001	0.481
Straight carapace width (mm) and emergence success (%)	<0.0001	0.587
Straight carapace length (mm) and emergence success (%)	<0.0001	0.479
Mass (g) and emergence success (%)	<0.0001	0.685

with higher mean temperatures produced hatchlings with thicker BDs (mean $p \leq 0.0001$, corr. = 0.777; maximum $p \leq 0.0001$, corr. = 0.453; 3 d mean $p \leq 0.0001$, corr. = 0.486). Hatchlings from late-season nests had significantly shorter SCLs than hatchlings from early- and mid-season nests ($\chi^2(2) = 14.086$, $p \leq 0.0009$; early vs. late: $p = 0.02$; early vs. mid: $p = 1$; mid vs. late: $p = 0.0009$; Table 5). Hatchlings from early-, mid-, and late-season nests differed in BD as well, where later nests had hatchlings with larger BDs ($\chi^2(2) = 32.153$, $p \leq 0.0001$; early vs. late: $p \leq 0.0001$; early vs. mid: $p \leq 0.02$; mid vs. late: $p \leq 0.0003$; Table 5). BCI of the hatchlings differed between early-, mid-, and late-season nests ($\chi^2(2) = 77.974$, $p \leq 0.0001$; early vs. late: $p \leq 0.0001$; early vs. mid: $p \leq 0.0001$; mid vs. late: $p \leq 0.01$; Table 5). Flipper length is also correlated with temperature ($p \leq 0.001$, corr. = -0.292), with hatchlings from nests with the highest maximum temperatures having shorter flipper lengths. Mid- and late-season hatchling flipper lengths differed from each other, where hatchlings from mid-season nests had longer flippers ($\chi^2(2) = 9.4202$, $p = 0.009$; early vs. late: $p = 0.46$; early vs. mid: $p = 0.31$; mid vs. late: $p = 0.007$; Table 5). Mid- and late-season hatchling masses also differed significantly from each other, where mid-season hatchlings weighed more ($\chi^2(2) = 10.533$, $p = 0.005$; early vs. late: $p = 0.74$; early vs. mid: $p = 0.12$; mid vs. late: $p = 0.004$). Mass (mean $p = 0.37$, corr. = -0.084; maximum $p = 0.20$, corr. = -0.120; 3 d mean $p = 0.51$, corr. = -0.061) and SCW (mean $p = 0.39$, corr. = -0.081; maximum $p = 0.10$, corr. = -0.153; 3 d mean $p = 0.16$, corr. = -0.132) did not correlate with mean nest incubation temperature (Table 5).

3.4. Impacts of temperature on performance

Incubation temperatures were negatively correlated with righting propensity score (mean temperature $p \leq 0.0001$, corr. = -0.509; maximum temperature $p \leq 0.0001$, corr. = -0.446; maximum 3 d mean temperature $p \leq 0.0001$, corr. = -0.478). Hatchlings incubating at higher temperatures struggled to right themselves; thus, late-season nests had significantly lower propensity scores ($\chi^2(2) = 45.045$, $p \leq 0.0001$; early vs. late: $p \leq 0.0001$; early vs. mid: $p = 0.84$; mid vs. late: $p \leq 0.0001$) than mid- and early-season nests (Fig. 3). While the righting propensity scores ranged from 0 to 6, 31% of all the hatchlings tested across the season could not right themselves even 1 time. The hatchlings unable to right themselves came largely from late-season, warmer nests; late nests had the lowest median score of 0, while mid and early nests had median scores of 5 and 6, respectively. The nest with the highest overall mean temperature of $32.5 \pm 1.6^\circ\text{C}$ had the lowest propensity score; only 1 of 10 of those hatchlings was able to right itself at all, and then only 1 time in 6 attempts.

The better-performing hatchlings came primarily from early- and mid-season nests, as late-season hatchlings in general were smaller and had greater

Table 5. Leatherback turtle (*Dermochelys coriacea*) hatchling morphometrics. Data represent median values (ranges in parentheses). Data with different letters indicate significant differences between groups in the same category ($p \leq 0.05$). n = 4 nests for each part of the nesting season. Maximum temperature was recorded in the last week of incubation for all groups

	Time of season		
	Early 27 Mar–18 Apr (29.0–30.1°C)	Mid 3–16 May (30.7–31.0°C)	Late 20 May–14 Jun (32.0–32.5°C)
Straight carapace length (mm)	60.6 ^a (55.6–64.2)	60.7 ^a (54.8–65.4)	58.8 ^b (52.6–63.3)
Straight carapace width (mm)	41.3 (35.6–43.6)	40.7 (34.8–43.5)	40.4 (34.9–43.9)
Mass (g)	43.9 ^{ab} (33.8–50.7)	45.1 ^a (38.5–50.5)	41.5 ^b (36.4–52.1)
Body depth (mm)	24.7 ^a (22.4–28.0)	25.3 ^b (22.8–28.1)	26.4 ^c (24.2–29.2)
Body condition index	2.0 ^a (1.7–2.4)	2.0 ^b (1.7–2.8)	2.1 ^c (1.7–3.1)
Average flipper length (mm)	53.9 ^{ab} (48.2–60.3)	55.2 ^a (49.8–58.9)	53.3 ^b (48.1–58.9)

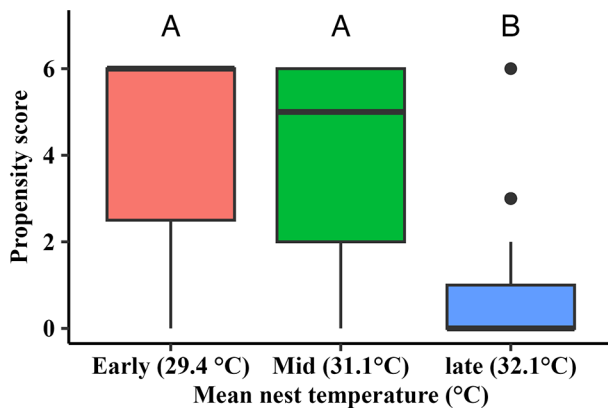


Fig. 3. Leatherback turtle (*Dermodochelys coriacea*) hatchling righting propensity score varies with temperature. Late-season nests (mean temperature of 32.1°C) had a significantly lower propensity score when compared to mid-season (31.1°C) and early-season (29.4°C) nests (Kruskal-Wallis chi-squared = 102.02, df = 2, $p < 2.2e^{-16}$). Sample size: early, n = 4 nests (38 hatchlings); mid, n = 4 nests (40 hatchlings); late, n = 4 nests (37 hatchlings). Dunn's test with Bonferroni adjustments results are shown as letters above each box. Medians not sharing the same letter are significantly different. Bar: median; box: 25th–75th percentile (IQR); whiskers: max./min. 1.5× IQR above/below box; dots: outliers

BDs (Table 5). Hatchlings having a wider ($p = 0.003$, corr. = 0.276) and longer ($p = 0.001$, corr. = 0.293) carapace and longer flippers ($p = 0.0001$, corr. = 0.347) were able to right themselves more quickly. Hatchlings that were smaller and/or had a larger BD ($p \leq 0.0001$, corr. = -0.440) struggled to right themselves (Table 6). Mean crawling speeds ranged from 0.008 to 0.092 $m s^{-1}$ (Fig. 4). There was no correlation between incubation temperature and crawling speed (mean temperature $p = 0.51$, corr. = -0.062; maximum temperature $p = 0.76$, corr. = -0.029; maximum 3 d mean temperature $p = 0.48$, corr. = -0.068) nor between crawling speed and hatchling size (Table 6). Crawling speed did not significantly differ between early, mid, and late nests ($\chi^2(2) = 2.01$, $p = 0.366$).

Table 6. Correlations between hatchling morphometrics and leatherback turtle (*Dermodochelys coriacea*) performance (righting response). All hatchlings from all 12 nests were included in these analyses (n = 115)

Variable	p	Correlation
Straight carapace length (mm)	<0.001	0.293
Straight carapace width (mm)	<0.003	0.277
Mass (g)	<0.001	0.294
Average flipper length (mm)	<0.0001	0.347
Body depth (mm)	<0.0001	-0.440
Body condition index	<0.0001	-0.365

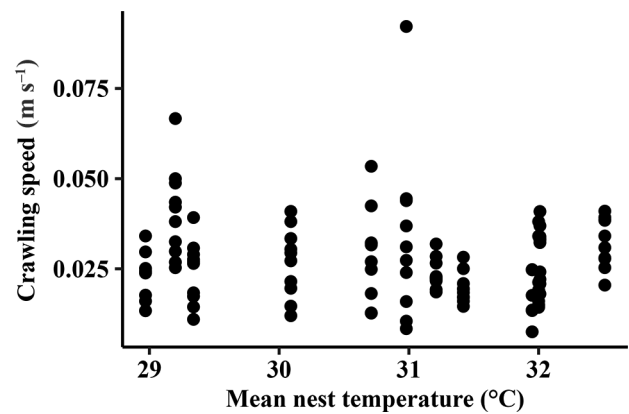


Fig. 4. Mean nest temperature did not have a significant effect on leatherback turtle (*Dermodochelys coriacea*) hatchling crawling speed. All hatchlings from all 12 nests were included in this analysis (n = 115)

4. DISCUSSION

This is the first study to examine the effects of incubation temperature on South Florida leatherback (*Dermodochelys coriacea*) hatchling performance. In this study, we found that, similar to other sea turtle species and as in leatherback turtles in other locations (Ackerman 1997, Booth et al. 2004, García-Grajales et al. 2019, Usategui-Martín et al. 2019), cooler nest temperatures resulted in longer incubation periods than warmer nest temperatures. Temperatures were correlated not only with incubation length but also with nest success and hatchling locomotor performance. This suggests that there could be a temperature sweet spot for incubation since the mid-season nests had both higher hatching and emergence success and better hatchling physical performance. This finding is consistent with previous works (Booth 2017; their Fig. 1). Further studies need to be conducted on leatherback turtles to confirm the finding in this study since this study only had a sample size of 12 nests.

4.1. Nest temperatures

In a concomitant study of loggerhead and green turtle nests at the same location, we found that leatherback turtle nests had lower mean nest temperatures than loggerhead and green nests (Seaman 2020). However, the maximum nest temperatures still reached as high as loggerhead and green nest temperatures (data not shown) (Seaman 2020). Leatherback turtle nest temperatures reached 36°C, which is thought in other species to be near the

upper critical temperature, even though their nest depths (top: 61 cm; bottom: 81.3 cm) are deeper than average loggerhead nest depths (top: 35 cm; bottom: 53 cm) on the same beach (Seaman 2020) and they begin nesting earlier in the season than loggerhead turtles. One study on leatherback nests in the West Indies showed slightly cooler nest temperatures, but this is most likely due to differing nest environments in the West Indies compared to the current South Florida nest environment (Mickelson & Downie 2010). Studies conducted in Costa Rica observed similar nest temperatures as those reported in this study and found that nest shading and precipitation impacted the nest temperatures (Santidrián Tomillo et al. 2009, 2014, Hill et al. 2015, Santidrián Tomillo et al. 2017, Swiggs et al. 2018). A more recent study on leatherback nests in Mexico found nest temperatures have increased over the years, and their recent nest temperatures are similar to our findings and to those of other recent studies on other sea turtle species (García-Grajales et al. 2019, Usategui-Martín et al. 2019, Fleming et al. 2020). Charles et al. (2023) recently reported similar leatherback mean nest temperatures in Grenada, West Indies, with highs also reaching above 36°C. These similarities between leatherback and loggerhead nest temperatures in Florida and elsewhere in the Caribbean suggest that all nest depths are susceptible to the impacts of increasingly higher environmental temperatures.

4.2. Nest success

Our results on hatching success and emergence success are consistent with previous work conducted over 10 yr (2002–2012) on Florida beaches, which reported hatching success was 41.2% and emergence success was 37.4% for leatherback turtle nests (Brost et al. 2015). These results are also consistent with studies on leatherback turtles in other locations (Santidrián Tomillo et al. 2009, 2014, Veelenturf et al. 2022). Studies in Costa Rica on leatherback turtle nests showed higher leatherback nest success due to precipitation, shading, and the moisture content of the sand, reflecting how the beach environment can alter nest success (Santidrián Tomillo et al. 2015, Swiggs et al. 2018, Rivas et al. 2019). In 2019 (the year of this study), there were 187 leatherback nests laid on the study beach, with nest success determined for 149 of them. Hatch success for all the found nests on Juno Beach was 44.7%, with emergence success at 37.3%; thus, the hatch and emergence

success reported here for both early- and late-season nests was similar to the study site as a whole, while mid-season nests performed better than the mean. Peak nest success occurred in nests with mean temperatures around 31.0°C (Fig. 2). These results are consistent with those reported for leatherbacks in Costa Rica (Santidrián Tomillo et al. 2017), with a peak in hatching success between 29.0 and 30°C. In South Carolina, loggerhead turtles had a peak hatch success when incubated at 29.0°C, indicating that while there might be an ideal temperature for sea turtle nest success, the specific temperature likely varies by location and/or species, as local adaptations may be present (Fisher et al. 2014, Santidrián Tomillo et al. 2017, Monsinjon et al. 2019, Bentley et al. 2020). It is interesting to see Florida leatherback turtles showing peak hatching and emergence success at 31.0°C but South Carolina loggerheads peaking at 29.0°C; this suggests that South Florida sea turtle hatchlings may be tolerant of the hotter and possibly drier summers of the sub-tropics (Henaghan 2018), as the temperatures seen in this study and for green and loggerhead turtles in other studies conducted in South Florida (Lolavar & Wyneken 2015, Henaghan 2018, Fleming et al. 2020) are above those seen in studies performed in cooler climates (Ischer et al. 2009, Fisher et al. 2014).

It should be noted that this study did utilize a small sample size, and there should be further studies to confirm this trend with larger sample sizes and on other beaches. The leatherback turtle nests in this study had an overall lower hatching success (45%) than the loggerhead (73%) and green (70%) sea turtles in the concomitant study (Seaman 2020), so even though maximum nest temperatures experienced in leatherback turtle nests were as high as those found in the nests of other species in South Florida, and may contribute to embryonic death, there must also be something else contributing to the low hatching success compared to green and loggerhead hatchlings. Previous studies have suggested that genetics, embryonic mortality due to disease, maternal health, and climatic conditions play a role in the low hatching and emergence success of leatherback turtles (Bell et al. 2004, Rafferty et al. 2011, Perrault et al. 2011, 2012, 2013, Patino-Martinez et al. 2012, Hill et al. 2019, Monsinjon et al. 2019, Charles et al. 2023).

4.3. Body morphology

Leatherback hatchlings that experienced hotter nest temperatures had a higher BCI, resulting from

smaller carapaces and a thicker BD. By convention, a higher BCI would suggest that the organism is in good health (Herbst & Jacobson 2003). However, the formula used to calculate BCI is typically used for larger turtles to suggest if an animal is emaciated (Herbst & Jacobson 2003). The body condition formula may not be the best way to measure hatchling body condition (Nishizawa & Joseph 2022), as it most likely largely represents the degree of yolk remaining. Leatherback hatchlings from this study had a larger BD when incubating at hotter temperatures. Nests incubating at hotter temperatures also had a shorter incubation period, which means embryo developmental time is shortened, and hatchlings are unable to convert as much of the yolk mass to body tissue growth. As with other studies (Booth et al. 2004, Mickelson & Downie 2010, Booth 2017), the lower conversion of yolk mass into body tissues causes hatchlings to have larger BDs. BCI may thus be a poor measure of hatchling health because hatchlings from warmer nests were shorter and of greater BD but also had the lowest emergence success and the poorest righting scores, which together mean fewer hatchlings from the hottest nests are likely to make it to the ocean. Mass was the 1 measurement with no correlation between leatherback hatchling morphometrics and nest temperature, consistent with previous research (Ischer et al. 2009, Read et al. 2012, Booth et al. 2013, Wood et al. 2014, Sim et al. 2015). It is thought that as egg yolk is absorbed and converted to tissue, the net body mass remains the same as those hatchlings where the yolk has not been fully absorbed (Booth & Astill 2001). Hotter leatherback nests similarly produced hatchlings with shorter flipper lengths in addition to shorter SCLs, which could also hinder their locomotion performance. Interestingly, similar incubation periods for leatherback, loggerhead, and green turtles on this beach imply similar cellular and organ differentiation rates, but the larger body mass of leatherback hatchlings must mean significantly faster growth rates (mass or size increase per unit time) in leatherback embryos.

While a correlation between hatchling size and incubation temperature has been shown in a number of studies in sea turtles, including leatherbacks (e.g. Ischer et al. 2009, Read et al. 2012, Wood et al. 2014, Fleming et al. 2020) and other turtle species (Rhen & Lang 1999, Steyermark & Spotila 2001), maternal influences including egg mass also play a role in hatchling size (Booth et al. 2013, Tezak et al. 2020). We did not measure egg mass in this study, so maternal influences cannot be ruled out, though in snap-

ping turtle hatchlings egg mass only explained 47% of the variation in hatchling mass, so egg mass is just one factor impacting hatchling size (Steyermark & Spotila 2001, Tezak et al. 2020). It seems unlikely, though not possible to rule out, that a sampling bias occurred due to smaller eggs being laid primarily in warmer nests and larger eggs in cooler nests.

4.4. Locomotor performance

Interestingly, locomotor performance did not show the same correlations with temperature as hatching and emergence success, indicating hatchlings can be good performers even if they come from nests with poor hatching and emergence success. The overall righting propensity score (mean score of 3) for leatherback hatchlings was lower than loggerhead (mean score of 5) and green (mean score of 5) scores in a parallel study on the same beach (Seaman 2020). Of the hatchlings tested, 70% of them were able to right themselves, which is somewhat lower than a study done on loggerhead sea turtles, where 83.5% were able to right themselves at least once (Henaghan 2018).

Nests incubating at mean nest temperatures of 32.0°C or above generally saw a decline in righting response, with the one exception of the nest with a mean incubation temperature of 31.2°C that also showed low performance. These findings are consistent with studies on other species, including loggerhead and green sea turtles (Fisher et al. 2014, Wood et al. 2014, Henaghan 2018), and leatherback hatchlings in Costa Rica (Rivas et al. 2019). In our study, maximum temperature appeared less important as an influence on performance than did overall mean nest temperature, as exemplified by 1 nest with a maximum temperature of 36.4°C but a mean of 30.7°C, which still exhibited better performance than nests with higher mean temperatures. A study conducted on olive ridley turtles *Lepidochelys olivacea* found hatchling performance to decrease if the nest experienced mean 3 d maximum incubation temperatures >34°C, which is consistent with our findings (Maulany et al. 2012b). The mean 3 d maximum has been found to be an indicator of thermal stress to embryos during development (Maulany et al. 2012a,b). Previous work on loggerhead and green turtles suggests that the greater the length of time at higher temperatures, the greater the impact on survival (Bladow & Milton 2019, Turkozan et al. 2021); a similar effect may occur with locomotion performance.

Leatherback hatchlings from this study crawled at speeds similar to those previously reported (Mickelson & Downie 2010). We found no correlation between crawling speed and temperature, unlike studies in other species which reported a negative correlation between crawling speed and temperature in both loggerhead and green hatchlings (Ischer et al. 2009, Booth et al. 2013, Sim et al. 2014, Wood et al. 2014, Henaghan 2018), and was also reported by Rivas et al. (2019) in leatherbacks. A study on loggerheads in Boca Raton, Florida, found loggerhead hatchling crawling speed declined with nests incubating at mean temperatures of 32.0°C and above (Henaghan 2018). In our study, the leatherback hatchlings crawled at similar speeds, regardless of incubation mean or maximum temperature, which suggests there are other factors influencing crawling performance. One factor that may influence terrestrial performance of leatherback hatchlings is their overall body morphology compared to the other species. Overall, leatherback hatchling locomotor performance is lower than that in loggerheads and greens in similar studies in South Florida; they righted themselves less well and crawled more slowly (Henaghan 2018, Fleming et al. 2020). While sea turtle body shape is a compromise between efficient locomotion in the water and sufficient locomotion on land, leatherback hatchlings may be less suited for terrestrial locomotion than either green or loggerhead hatchlings. The results may have been different if we had utilized performance tests in the water (i.e. swimming, self-righting in a bucket of water). Studies on leatherback hatchling locomotion and energetics in water would be beneficial since sea turtles spend the majority of their life in the sea, and leatherbacks are more pelagic than other species (Musick & Limpus 1996).

Overall, the most significant findings of this study were that leatherback nest temperatures potentially influence the development of hatchling morphology, and that hatchling morphology and performance are correlated. Leatherback nests laid later in the season, which overlap in time with the early part of loggerhead nesting in South Florida, can reach equally high mean and maximum temperatures, and high temperatures result in low hatching and emergence success and poor physical performance; the sweet spot of incubation temperatures for these nests appears to be around 31.0°C. While leatherback turtle nests are laid in the cooler months in South Florida and are deeper than the nests of other species, temperatures can still rise surprisingly high, and further studies should investigate the cause. Thus, increasing temperatures due to climate change pose a sig-

nificant threat to a species that already has lower nest success than other species which share the same nesting beaches.

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LITERATURE CITED

- Ackerman RA (1997) The nest environment and the embryonic development of sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, Vol 1. CRC Press, Boca Raton, FL, p 83–106
- ✦ Bandimere A, Paladino FV, Spotila JR, Panagopoulou A, Diéguez-Uribeondo J, Santidrián Tomillo P (2021) Effects of egg mass and local climate on morphology of East Pacific leatherback turtle *Dermochelys coriacea* hatchlings in Costa Rica. *Mar Ecol Prog Ser* 669:191–200
- ✦ Bell BA, Spotila JR, Paladino FV, Reina RD (2004) Low reproductive success of leatherback turtles, *Dermochelys coriacea*, is due to high embryonic mortality. *Biol Conserv* 115:131–138
- ✦ Bentley BP, Stubbs JL, Whiting SD, Mitchell NJ (2020) Variation in thermal traits describing sex determination and development in Western Australian sea turtle populations. *Funct Ecol* 34:2302–2314
- Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. *Ecol Appl* 10:269–282
- ✦ Bladow R, Milton S (2019) Embryonic mortality in green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtle nests increases with cumulative exposure to elevated temperatures. *J Exp Mar Biol Ecol* 518:151180
- ✦ Bolten AB, Crowder LB, Dodd MG, Macpherson SL and others (2011) Quantifying multiple threats to endangered species: an example from loggerhead sea turtles. *Front Ecol Environ* 9:295–301
- ✦ Booth DT (2017) Influence of incubation temperature on sea turtle hatchling quality. *Integr Zool* 12:352–360
- ✦ Booth DT, Astill K (2001) Incubation temperature, energy expenditure and hatchling size in the green turtle (*Chelonia mydas*), a species with temperature-sensitive sex determination. *Aust J Zool* 49:389–396
- ✦ Booth DT, Dunstan A (2018) A preliminary investigation into the early embryo death syndrome (EEDS) at the world's largest green turtle rookery. *PLOS ONE* 13:e0195462
- ✦ Booth DT, Burgess E, McCosker J, Lanyon JM (2004) The influence of incubation temperature on post-hatching fitness characteristics of turtles. *Int Congr Ser* 1275: 226–233
- ✦ Booth DT, Feeney R, Shibata Y (2013) Nest and maternal origin can influence morphology and locomotor performance of hatchling green turtles (*Chelonia mydas*) incubated in field nests. *Mar Biol* 160:127–137
- Broderick AC, Godley BJ, Hays GC (2001) Metabolic heating and the prediction of sex ratios for green turtles (*Chelonia mydas*). *Physiol Biochem Zool* 74:161–170

- Brost B, Witherington B, Meylan A, Leone E, Ehrhart L, Bagley D (2015) Sea turtle hatchling production from Florida (USA) beaches, 2002–2012, with recommendations for analyzing hatching success. *Endang Species Res* 27:53–68
- Carthy RR, Foley AM, Matsuzawa Y (2003) Incubation environment of loggerhead turtle nests: effects on hatching success and hatchling characteristics. In: Bolten AB, Witherington BE (eds) *Loggerhead sea turtles*. Smithsonian Institution Press, Washington, DC, p 144–153
- Charles KE, Morrall CE, Edwards JJ, Carter KD, Afema JA, Butler BP, Marancik DP (2023) Environmental and nesting variables associated with Atlantic leatherback sea turtle (*Dermochelys coriacea*) embryonic and hatching success rates in Grenada, West Indies. *Anim* 13:685
- Conover WJ (1999) *Practical nonparametric statistics*, 3rd edn. John Wiley & Sons, New York, NY
- Davenport J (1987) Locomotion in hatchling leatherback turtles (*Dermochelys coriacea*). *J Zool* 212:85–101
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672
- Erb V, Wyneken J (2019) Nest-to-surf mortality of loggerhead sea turtle (*Caretta caretta*) hatchlings on Florida's east coast. *Front Mar Sci* 6:1–10
- Fisher LR, Godfrey MH, Owens DW (2014) Incubation temperature effects on hatchling performance in the loggerhead sea turtle (*Caretta caretta*). *PLOS ONE* 9:e114880
- Fleming KA, Perrault JR, Stacy NI, Copenrath CM, Gainsbury AM (2020) Heat, health and hatchlings: associations of *in situ* nest temperatures with morphological and physiological characteristics of loggerhead sea turtle hatchlings from Florida. *Conserv Physiol* 8:coaa046
- Florida Fish and Wildlife Conservation Commission (2016) *Marine turtle conservation handbook*. FWC, Tallahassee, FL
- García-Grajales J, Meraz Hernando JF, Arcos García JL, Ramírez Fuentes E (2019) Incubation temperatures, sex ratio and hatching success of leatherback turtles (*Dermochelys coriacea*) in two protected hatcheries on the central Mexican coast of the eastern tropical Pacific Ocean. *Anim Biodivers Conserv* 42:143–152
- Garrett K, Wallace BP, Garner J, Paladino FV (2010) Variations in leatherback turtle nest environments: consequences for hatching success. *Endang Species Res* 11:147–155
- Hamann M, Fuentes MMPB, Ban NC, Mocellin VJL (2013) Climate change and marine turtles. In: Wyneken J, Lohmann KJ, Musick JA (eds) *The biology of sea turtles*, Vol 3. CRC Press, Boca Raton, FL, p 353–378
- Henaghan C (2018) Incubation temperature effects on loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtle hatchling vigor. MSc thesis, Florida Atlantic University, Boca Raton, FL
- Hendrickson JR (1958) The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Proc Zool Soc Lond* 130:455–535
- Herbst LH, Jacobson ER (2003) Practical approaches for studying sea turtle health and disease. In: Musick JA, Lutz PL, Wyneken J (eds) *The biology of sea turtles*, Vol 2. CRC Press, Boca Raton, FL, p 385–410
- Hill JE, Paladino FV, Spotila JR, Tomillo PS (2015) Shading and watering as a tool to mitigate the impacts of climate change in sea turtle nests. *PLOS ONE* 10:e0129528
- Hill K, Stewart KM, Rajeev S, Conan A, Dennis MM (2019) Pathology of leatherback sea turtle (*Dermochelys coriacea*) embryos and hatchlings from nests in St. Kitts, West Indies (2015–16). *J Wildl Dis* 55:782–793
- Ingle DN, Meredith TL, Perrault JR, Wyneken J (2021) Two heads are not always better than one: craniofacial and axial bifurcation in cheloniid embryos and hatchlings (*Chelonia mydas* and *Caretta caretta*). *J Morphol* 282:1233–1244
- IPCC (2014) *Climate change 2014: synthesis report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva
- Ischer T, Ireland K, Booth DT (2009) Locomotion performance of green turtle hatchlings from the Heron Island rookery, Great Barrier Reef. *Mar Biol* 156:1399–1409
- Kaska Y, Downie R, Tippett R, Furness RW (1998) Natural temperature regimes for loggerhead and green turtle nests in the eastern Mediterranean. *Can J Zool* 76:723–729
- Kobayashi S, Wada M, Fujimoto R, Kumazawa Y, Arai K, Watanabe G, Saito T (2017) The effects of nest incubation temperature on embryos and hatchlings of the loggerhead sea turtle: implications of sex difference for survival rates during early life stages. *J Exp Mar Biol Ecol* 486:274–281
- Lolavar A, Wyneken J (2015) Effect of rainfall on loggerhead turtle nest temperatures, sand temperatures and hatchling sex. *Endang Species Res* 28:235–247
- Maloney JE, Darian-smith C, Takahashi Y, Limpus CJ (1990) The environment for development of the embryonic loggerhead turtle (*Caretta caretta*) in Queensland. *Copeia* 1990:378–387
- Matsuzawa Y, Sato K, Sakamoto W, Bjorndal KA (2002) Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. *Mar Biol* 140:639–646
- Maulany RI, Booth DT, Baxter GS (2012a) Emergence success and sex ratio of natural and relocated nests of olive ridley turtles from Alas Purwo National Park, East Java, Indonesia. *Copeia* 738–747
- Maulany RI, Booth DT, Baxter GS (2012b) The effect of incubation temperature on hatchling quality in the olive ridley turtle, *Lepidochelys olivacea*, from Alas Purwo National Park, East Java, Indonesia: implications for hatchery management. *Mar Biol* 159:2651–2661
- Mickelson LE, Downie JR (2010) Influence of incubation temperature on morphology and locomotion performance of leatherback (*Dermochelys coriacea*) hatchlings. *Can J Zool* 88:359–368
- Miller JD (1985) Embryology of marine turtles. In: Gans C, Billett F, Maderson PFA (eds) *Biology of the Reptilia*, Vol 14. Wiley-Interscience, New York, NY, p 269–328
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, Vol 1. CRC Press, Boca Raton, FL, p 64–69
- Miller JD (1999) Determining clutch size and hatching success. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) *Research and management techniques for the conservation of sea turtles*. IUCN/SSC Mar Turtle Spec Group Publ No. 4
- Monsinjon JR, Wyneken J, Rusenko K, López-Mendilaharsu M and others (2019) The climatic debt of loggerhead sea turtle populations in a warming world. *Ecol Indic* 107:105657

- Musick JA, Limpus C (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, Vol 1. CRC Press, Boca Raton, FL, p 137–164
- ✦ Nishizawa H, Joseph J (2022) Differences in the morphological body condition index of sea turtles between species and size classes. *J Mar Biol Assoc UK* 102:479–485
- Northwest Atlantic Leatherback Working Group (2018) Northwest Atlantic leatherback turtle (*Dermodochelys coriacea*) status assessment. Tech Rep No. 16, Wider Caribbean Sea Turtle Conservation Network (WIDECAST), Godfrey, IL
- ✦ Patino-Martinez J, Marco A, Quiñones L, Hawkes L (2012) A potential tool to mitigate the impacts of climate change to the Caribbean leatherback sea turtle. *Glob Change Biol* 18:401–411
- ✦ Perrault J, Wyneken J, Thompson LJ, Johnson C, Miller DL (2011) Why are hatching and emergence success low? Mercury and selenium concentrations in nesting leatherback sea turtles (*Dermodochelys coriacea*) and their young in Florida. *Mar Pollut Bull* 62:1671–1682
- ✦ Perrault JR, Miller DL, Eads E, Johnson C, Merrill A, Thompson LJ, Wyneken J (2012) Maternal health status correlates with nest success of leatherback sea turtles (*Dermodochelys coriacea*) from Florida. *PLOS ONE* 7: e31841
- ✦ Perrault JR, Miller DL, Garner J, Wyneken J (2013) Mercury and selenium concentrations in leatherback sea turtles (*Dermodochelys coriacea*): population comparisons, implications for reproductive success, hazard quotients and directions for future research. *Sci Total Environ* 463–464: 61–71
- R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Rafferty AR, Santidrián Tomillo P, Spotila JR, Paladino FV, Reina RD (2011) Embryonic death is linked to maternal identity in the leatherback turtle (*Dermodochelys coriacea*). *PLOS ONE* 6:e21038
- ✦ Read T, Booth DT, Limpus CJ (2012) Effect of nest temperature on hatchling phenotype of loggerhead turtles (*Caretta caretta*) from two South Pacific rookeries, Mon Repos and la Roche Percée. *Aust J Zool* 60:402–411
- ✦ Rhen T, Lang JW (1999) Temperature during embryonic and juvenile development influences growth in hatchling snapping turtles, *Chelydra serpentina*. *J Therm Biol* 24: 33–41
- ✦ Rivas ML, Esteban N, Marco A (2019) Potential male leatherback hatchlings exhibit higher fitness which might balance sea turtle sex ratios in the face of climate change. *Clim Change* 156:1–14
- ✦ Salmon M, Higgins B, Stewart J, Wyneken J (2015) The ontogeny of morphological defenses in Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) sea turtles. *J Morphol* 276:929–940
- ✦ Santidrián Tomillo P, Suss JS, Wallace BP, Magrini KD, Blanco G, Paladino FV, Spotila JR (2009) Influence of emergence success on the annual reproductive output of leatherback turtles. *Mar Biol* 156:2021–2031
- ✦ Santidrián Tomillo P, Paladino FV, Suss JS, Spotila JR (2010) Predation of leatherback turtle hatchlings during the crawl to the water. *Chelonian Conserv Biol* 9: 18–25
- ✦ Santidrián Tomillo P, Oro D, Paladino F V, Piedra R, Sieg AE, Spotila JR (2014) High beach temperatures increased female-biased primary sex ratios but reduced output of female hatchlings in the leatherback turtle. *Biol Conserv* 176:71–79
- ✦ Santidrián Tomillo P, Saba VS, Lombard CD, Valiulis JM and others (2015) Global analysis of the effect of local climate on the hatchling output of leatherback turtles. *Sci Rep* 5:16789
- ✦ Santidrián Tomillo P, Fonseca L, Paladino FV, Spotila JR (2017) Are thermal barriers 'higher' in deep sea turtle nests? *PLOS ONE* 12:e0177256
- Seaman HA (2020) The impacts of nest microenvironment on sea turtle hatchling performance and their responses to thermal stress. MSc thesis, Florida Atlantic University, Boca Raton, FL
- ✦ Sim EL, Booth DT, Limpus CJ (2014) Non-modal scute patterns, morphology, and locomotor performance of loggerhead (*Caretta caretta*) and flatback (*Natator depressus*) turtle hatchlings. *Copeia* 63–69
- ✦ Sim EL, Booth DT, Limpus CJ (2015) Incubation temperature, morphology and performance in loggerhead (*Caretta caretta*) turtle hatchlings from Mon Repos, Queensland, Australia. *Biol Open* 4:685–692
- ✦ Standora EA, Spotila JR (1985) Temperature dependent sex determination in sea turtles. *Copeia* 1985:711–722
- ✦ Stewart KR, Martin KJ, Johnson C, Desjardin N, Eckert SA, Crowder LB (2014) Increased nesting, good survival and variable site fidelity for leatherback turtles in Florida, USA. *Biol Conserv* 176:117–125
- ✦ Steyermark AC, Spotila JR (2001) Effects of maternal identity and incubation temperature on hatching and hatchling morphology in snapping turtles, *Chelydra serpentina*. *Copeia* 2001:129–135
- ✦ Swiggs J, Paladino FV, Spotila JR, Tomillo PS (2018) Depth of the drying front and temperature affect emergence of leatherback turtle hatchlings from the nest. *Mar Biol* 165: 1–10
- ✦ Tanabe LK, Steenacker M, Rusli MU, Berumen ML (2021) Implications of nest relocation for morphology and locomotor performance of green turtle (*Chelonia mydas*) hatchlings. *Ocean Coast Manage* 207:105591
- ✦ Telemeco RS, Warner DA, Reida MK, Janzen FJ (2013) Extreme developmental temperatures result in morphological abnormalities in painted turtles (*Chrysemys picta*): a climate change perspective. *Integr Zool* 8: 197–208
- ✦ Tezak B, Bentley B, Arena M, Mueller S, Snyder T, Sifuentes-Romero I (2020) Incubation environment and parental identity affect sea turtle development and hatchling phenotype. *Oecologia* 192:939–951
- ✦ Turkozan O, Alpanidou V, Yilmaz C, Mazaris AD (2021) Extreme thermal conditions in sea turtle nests jeopardize reproductive output. *Clim Change* 167:1–16
- ✦ Usategui-Martín A, Liria-Loza A, Miller JD, Medina-Suárez M, Jiménez-Bordón S, Pérez-Mellado V, Montero D (2019) Effects of incubation temperature on hatchling performance and phenotype in loggerhead sea turtle *Caretta caretta*. *Endang Species Res* 38:45–53
- ✦ Veelenturf CA, Sinclair EM, Leopold P, Paladino FV, Honarvar S (2022) The effects of nest location and beach environment on hatching success for leatherback (*Dermodochelys coriacea*) and green (*Chelonia mydas*) sea turtles on Bioko Island, Equatorial Guinea. *Mar Biol* 169:56
- ✦ Wallace BP, Sotherland PR, Santidrián Tomillo P, Reina RD, Spotila JR, Paladino FV (2007) Maternal investment in

reproduction and its consequences in leatherback turtles. *Oecologia* 152:37–47

✈ Wood A, Booth DT, Limpus CJ (2014) Sun exposure, nest temperature and loggerhead turtle hatchlings: implications for beach shading management strategies at sea turtle rookeries. *J Exp Mar Biol Ecol* 451:105–114

Wyneken J (1997) Sea turtle locomotion: mechanisms, behavior, and energetics. In: Lutz PL, Musick JA (eds)

The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 165–198

✈ Zbinden JA, Margaritoulis D, Arlettaz R (2006) Metabolic heating in Mediterranean loggerhead sea turtle clutches. *J Exp Mar Biol Ecol* 334:151–157

✈ Zimm R, Bentley BP, Wyneken J, Moustakas-Verho JE (2017) Environmental causation of turtle scute anomalies *in ovo* and *in silico*. *Integr Comp Biol* 57:1303–1311

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