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Year-to-year variation in core body temperatures of nesting leatherback and hawksbill sea turtles

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Using non-contact infrared thermometers, the surface temperatures of freshly laid eggs of sea turtles were measured as proxies of core body temperatures while they were nesting. Data were accumulated over seven consecutive nesting seasons for two species with contrasting lifestyles – leatherbacks *Dermochelys coriacea*, the largest, which are anatomically adapted to migrate between tropical breeding sites to cold temperate waters, and the smaller hawksbills *Eretmochelys imbricata* that are generally confined to the tropics and sub-tropics. Leatherbacks ranged between 28.7 °C and 32.5 °C (30.9 °C ± 0.6 °C; mean ± standard deviation) and hawksbills 26.3 °C to 32.0 °C (29.2 °C ± 0.8 °C), with year-to-year variations in temperatures in populations of both species (year mean 30.4 °C to 31.5 °C in leatherbacks), hawksbills the more so (28.1 °C to 30.3 °C). These differences will likely be modified by both natural seasonal variations, anthropogenic changes in ocean temperatures and variabilities in currents and water temperatures local to nesting beaches. Such diversities in body temperatures of nesting turtles are pertinent to predicting environmental tolerances, reproductive success and nest site selection, and could contribute to predicting which rookeries may remain viable or not as oceans warm.

Keywords: Dermochelys coriacea, *Eretmochelys imbricata*, core body temperatures, egg surface temperatures, oviposition

INTRODUCTION

Sea turtles range across oceans for feeding and breeding, seasonal migrations that expose them to a broad range of environmental temperatures that are now undergoing anthropogenic change. Those that encounter the greatest temperature ranges are adult leatherback turtles *Dermochelys coriacea,* which travel from the tropics where they mate and nest, to cold temperate waters where many feed between nesting seasons (Ferraroli et al., 2004; Hays et al., 2004; James et al., 2005; Caut et al., 2008; Fossette et al., 2014). Most other sea turtle species, such as hawksbills *Eretmochelys imbricata*, are mainly confined to tropical and subtropical waters, and do not encounter similar extremes. Leatherback and hawksbill turtles can be sympatric when their nesting seasons co-incide, then experiencing similar temperature regimes, albeit with contrasting temperature exposures at other times.

Rising anthropogenic global temperatures are leading to increasing concerns about how and where sea turtles may successfully nest, or indeed survive, in the seas around, and migration routes to, their rookeries (Tomillo et al., 2020; Hays et al., 2021; Okuyama et al., 2021; Hays et al., 2022; Robinson et al., 2022; Chen et al., 2025; Lettrich et al., 2025). There are already predictions that oceans may warm to a degree that may be intolerable to sea turtles, the well-insulated leatherbacks therefore being at particular risk (Dudley & Porter, 2014; Dudley et al., 2016; Patricio et al., 2021). Meanwhile, rising sand temperatures on nest beaches are increasingly thought to be to the detriment of egg survival (Howard et al., 2014; Tomillo et al., 2017; Jensen et al., 2018; Gammon et al., 2020; Bandimere et al., 2021; Turkozan et al., 2021), and, through temperature-dependent sex determination during development in chelonians, deemed already to be affecting sex ratios of hatchlings such that an excess of females appears (Jensen et al., 2018; Patricio et al., 2021; Laloe & Hays, 2023).

Increased temperatures of beaches may or may not be paralleled by increases in adjacent seas - changes in ocean temperatures may de-stabilise sea currents and eddies that may thereby change the temperatures, flow rates and directions of waters local to nesting beaches, in addition to sea level rise (Hu et al., 2020; Garreaud et al., 2021; Beech et al., 2022; Guo et al., 2022; Peng et al., 2022). Changes in ocean currents caused by global warming may therefore bring warmer or cooler currents to increasingly hot beaches. While sea turtles exhibit return to their natal beaches to a strong but not absolute degree (Rees et al., 2016; Lohmann & Lohmann, 2019; Patricio et al., 2021), were they to be influenced in choosing a nesting beach partly on the temperatures of the waters they traverse during migration, or in which they congregate before heading to shore, then increasing local water temperatures may affect selection of nesting sites and phenology.

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The degree to which sea turtles will change, or already are changing their nest sites and migration routes in response to global warming is receiving attention (Girondot et al., 2006; Neeman et al., 2015; Patricio et al., 2021; Laloe & Hays, 2023; Fuentes et al., 2024; Kynoch et al., 2024; Rickwood et al., 2025). Predicting which beaches and the sea approaches to them are to become reproductively unstable, or simply avoided by turtles, will require an understanding of how they respond to increasingly variable ocean conditions. As global warming proceeds, nesting beaches may also oscillate between being non-viable one year to viable the next. Work at several sites has been following seasonal and annual fluctuations in beach temperatures, and temperatures within nests, including studying the gradient of temperatures vertically through nests, of several species of sea turtle (Sullivan et al., 2022; Veelenturf et al., 2022; Charles et al., 2023; Laloe & Hays, 2023). Meanwhile, satellite-based data on sea surface temperatures (SSTs) are informative of changing ocean conditions, although this is complicated by differences between surface and bulk sub-surface water (Amaya et al., 2020; Chen et al., 2021; Guo et al., 2022; Liu et al., 2022; Peng et al., 2022; Luo et al., 2023; Tang et al., 2023). Moreover, given the complexity of water movements in inshore waters, it will likely be difficult to gauge the temperatures of waters in which turtles sojourn before landing to nest, and how they vary through a season or from year to year.

One way of appreciating the exposure of sea turtles to sea temperature changes is to measure the core body temperatures of nesting females soon after they emerge from the sea, sampled over several seasons. These have been measured using potentially harmful invasive techniques, but latterly by measuring freshly laid eggs (summarised in Burns et al., 2015). This assumes that eggs in the oviduct thermally equilibrate to the internal tissues of a turtle, such that measuring the temperatures of eggs within a second or two of laying should act as a proxy for a female’s core body temperature. This can be done non-destructively by using infrared-based thermometers, which allows rapid measurement of large numbers of eggs of many females in order to obtain reliable mean values for each individual easily in the field.

This report extends previous data on egg surface temperatures gathered over two years (Burns et al., 2015) to build a seven-year survey of core body temperatures of two species of sea turtle with contrasting migratory propensities and body sizes – leatherback and hawksbill turtles – whose nesting seasons are near-contemporaneous and in the same part of the Caribbean Sea. We found diversity in body temperatures of individuals in both species, most noticeably in hawksbills, and distinct year-to-year variability in both species that were again more notable in hawksbills.

MATERIALS & METHODS

Study sites and animals

Observations of nesting leatherback sea turtles *D. coriacea* were made on Fishing Pond beach on the east coast of Trinidad (approximately 10° 36'00.0" N, 61° 01'12.0" W), and hawksbill sea turtles *E. imbricata* on Campbleton and Hermitage bays in the northeast of Tobago (approximately 11° 19'03.9" N, 60° 34'02.1" W). The sites are approximately 95 km apart, and both islands are exposed to the North Equatorial Current flowing from the east. Measurements of egg temperatures were made during early June to early August for both species between 2013 to 2019, the measurements beginning approximately at the peak of nesting activity of each species such that the two species were being recorded at the same phases of the nesting season over the same two months of the year.

Measurement of core body temperatures

The surface temperature of freshly laid eggs was used as a non-contact proxy of core body temperature as previously described (Burns et al., 2015). Measurements were taken using Fluke 62 Max Plus handheld dual laser spot-guided infrared thermometers (spectral range 8–14 µm, accuracy ±1 °C or 1%, thermal sensitivity/resolution 0.1 °C) set to an emissivity of 0.98, which is a value taken as typical for emissivity of biological tissues (McCafferty et al., 2013; Rowe et al., 2013; Mortola, 2013). Infrared thermometers were calibrated against a thermocouple and a mercury thermometer of 0.1 °C sensitivity. For leatherbacks, sand was removed from the edges of the nest hole to gain access to the eggs. For hawksbills, sand was removed from the rear of the nest cavity to the same end. In both cases this could be done with minimal or usually no contact with the animal. Measurements were taken at about 20 cm from the eggs surface, and only on eggs that were clearly observed to be freshly laid, and had no sand attached to the side which was being measured. Measurements were taken within one or two seconds of emergence of an egg to avoid any significant cooling by evaporation. The values for 2013 and 2014 are the same as those we reported previously (Burns et al., 2015).

Sea surface temperatures (SSTs)

SSTs were obtained from satellite-based data (https://oceanwatch.pifsc.noaa.gov/erddap/griddap/CRW_sst_v3_1.html), using the latitude and longitude settings of 10.60559; 298.97712 for the Trinidad site of leatherback turtle nesting (Fishing Pond beach), and 11.31774; 299.43274 for the Tobago hawksbill site (Hermitage and Campbleton beaches). These co-ordinates were set for approximately 200 m offshore of the nesting beaches.

Statistical procedures

Data were analysed and plotted using Microcal ORIGIN 2022 and MS Excel softwares. Analysis of variance analyses (ANOVA) were carried out using the Tukey procedure using ORIGIN.

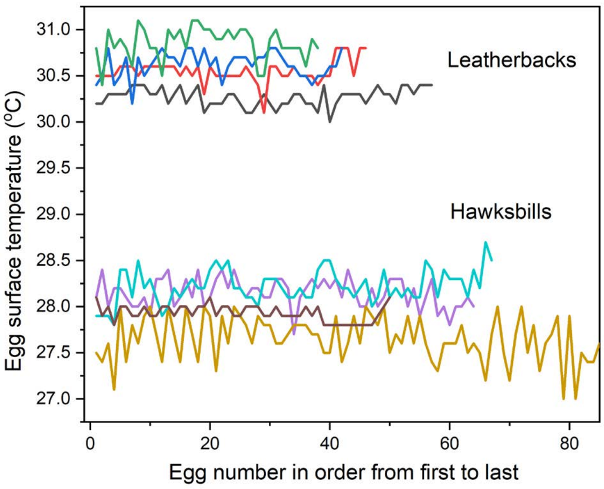
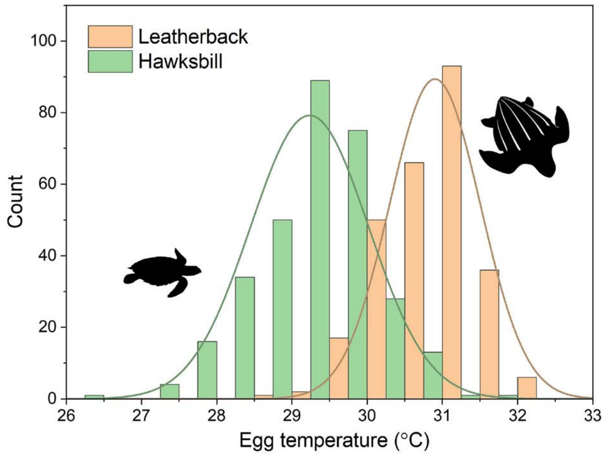


Figure 1. Consistency of egg surface temperature from beginning to end of laying in leatherback and hawksbill turtles. Egg temperatures in egg order laid from first to last. Eggs are laid in batches, and the surface temperatures were recorded from the first egg only in a batch that was accessible and clean of sand. The graph is from four individual leatherbacks and four hawksbills recorded during the 2018 season.



Species	N	Mean °C	Standard deviation	SE of mean	Variance	Mode	Median
Leatherback	271	30.90	0.61	0.04	0.37	30.40	31.00
Hawksbill	312	29.23	0.79	0.04	0.62	29.40	29.32

Figure 2. Core body temperature differences between leatherback and hawksbill turtles. Cumulative egg temperature measurements of the two species accumulated over the seven field seasons 2013–2019 inclusive. Data were obtained from 271 nesting instances of leatherback turtles and 312 hawksbills, and a Gaussian distribution is fitted to them separately. Descriptive statistics for the data for each species are given below the figure. Note that the variance for leatherbacks is almost half that for hawksbills. Turtle silhouettes from http://phylopic.org/.

RESULTS

Body temperatures of leatherback and hawksbill turtles

Over the seven nesting seasons 2013 to 2019, 271 nesting events by leatherback and 312 by hawksbill turtles were recorded. The egg temperatures used for each turtle sampled were averages of up to about 80 or more eggs measured per turtle, depending on accessibility. For many of the turtles, egg surface temperatures were recorded from the first to the last laid which allowed us to check whether their temperatures varied during laying, such as might occur with differential proximities between body core and surface. This revealed very little differences in the temperatures recorded during an individual animal's nesting, with no signs of overall increases or decreases with time (Fig. 1).

Pooling the data from all seven years yields temperature frequency distributions for each species as shown in Figure 2. Mean core body temperatures for leatherbacks and hawksbills were 30.9 °C and 29.2 °C, respectively, with the medians and modes approximately 1.7 °C apart, and the variance for hawksbills being approximately double that for leatherbacks (see statistical summary in Figure 2). These temperature values are similar in range to those reported by others for leatherbacks when in their nesting areas, using both invasive and non-invasive methods (summarised in Burns et al., 2015).

Year to year variation in sea turtle body temperatures

Inspection of the data for the separate nesting seasons indicates distinct variation from year to year in both species, though greater for hawksbills (Fig. 3). There were

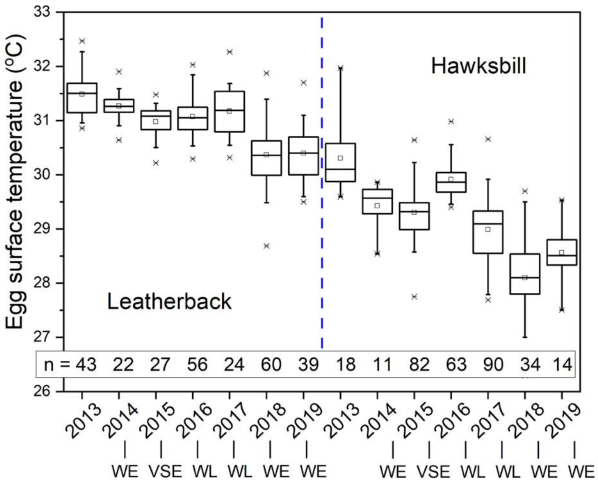


Figure 3. Differences in core body temperatures of leatherback and hawksbill turtles from egg surface temperatures over seven nesting seasons. Boxes represent 25 and 75% interquartile ranges; horizontal lines through boxes indicate medians; squares indicate the means; whiskers show 5th and 95th percentiles; and crosses indicate the maximum and minimum values. The number of turtle nestings observed in each year are as indicated (n). WE = Weak El Niño; VSE = Very Strong El Niño, WL = Weak La Niña; other years were classified as neutral (https://ggweather.com/enso/oni.htm).

Table 1. Statistical comparison of year-to-year variation in core body temperatures of leatherback and hawksbill sea turtles. Analysis of variance analysis with the Tukey procedure set at 95% confidence. Grouping tables where means that do not share a letter are significantly different ($p < 0.05$). Note that year-to-year disparities are more frequent in hawksbills than leatherback turtles.

Leatherback turtles

Year	N	Mean	Grouping		
2013	43	31.49	A		
2014	22	31.27	A	B	
2017	24	31.17	A	B	
2016	56	31.07		B	
2015	27	30.98		B	
2019	39	30.40			C
2018	60	30.37			C

Hawksbill turtles

Factor	N	Mean	Grouping					
2013	18	30.31	A					
2016	63	29.91	A	B				
2014	11	29.43		B	C	D		
2015	82	29.31			C			
2017	90	28.99				D	E	
2019	14	28.56					E	F
2018	34	28.10						F

statistically significant increases or decreases, or none, in core temperatures from year to year for both species, and year-to-year fluctuations were greater in hawksbills than leatherbacks (Fig. 3; Table 1), potentially due to a combination of intrinsic differences in the species in body temperature regulation and differences in the waters they occupied before coming ashore. Figure 3 also shows that the overall pattern of mean core temperature increases or decreases from year-to-year were similar between the two species, albeit on different scales, dampened in leatherbacks. When the yearly values for each species are plotted against one another there is a good correlation between the two (Fig. 4A). Figure 4B shows that sea temperatures at the Trinidad and Tobago nesting sites are closely correlated, and Figure 4C shows that rises and falls in overall egg temperatures from year to year roughly follow changes in averaged sea temperatures, for hawksbills in particular, and that the body temperatures of both species are above recorded SSTs.

Regarding year-to-year changes in sea temperatures during nesting seasons, Figures 5A and 5C show SSTs about 200 m offshore from the nesting beaches; Figures 5B and 5D show mathematically-smoothed data. The day-to-day variation is considerable, presumably due to regional climatic effects, currents and tides controlled by the lunar cycle. Our observations at both sites covered the periods roughly from the beginning of June to the end of July corresponding with temperature peaks.

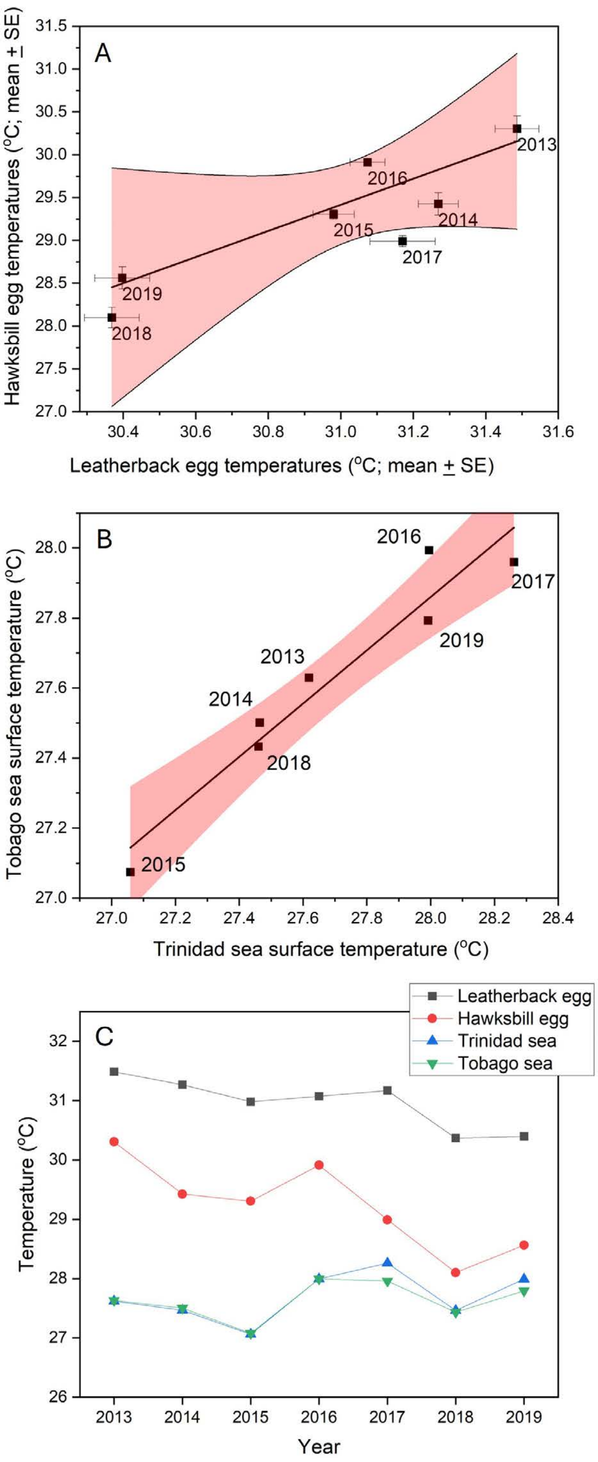


Figure 4. Correlation between female leatherback and hawksbill turtle egg temperatures at the two nesting areas. **A.** Average temperatures for all the eggs of each species measured for each year ± standard errors. The linear line fit values are equation $y = 1.55x - 18.77$; $R^2 = 0.76$ and the shaded area represents the 95% confidence intervals. **B.** Comparison of sea temperatures between the Trinidad and Tobago sites. Data points are the averages of daily sea surface temperatures taken approximately 200 m offshore at between June 15th and July 15th of each year. Linear fitting yields slope $y = 0.76x + 6.5669$; $R^2 = 0.93$; the coloured band covers the 95 % confidence internals. **C.** Comparison of the mean egg temperatures of the two species of turtle versus the average of sea surface temperatures taken between 15 June-15 July of each year.

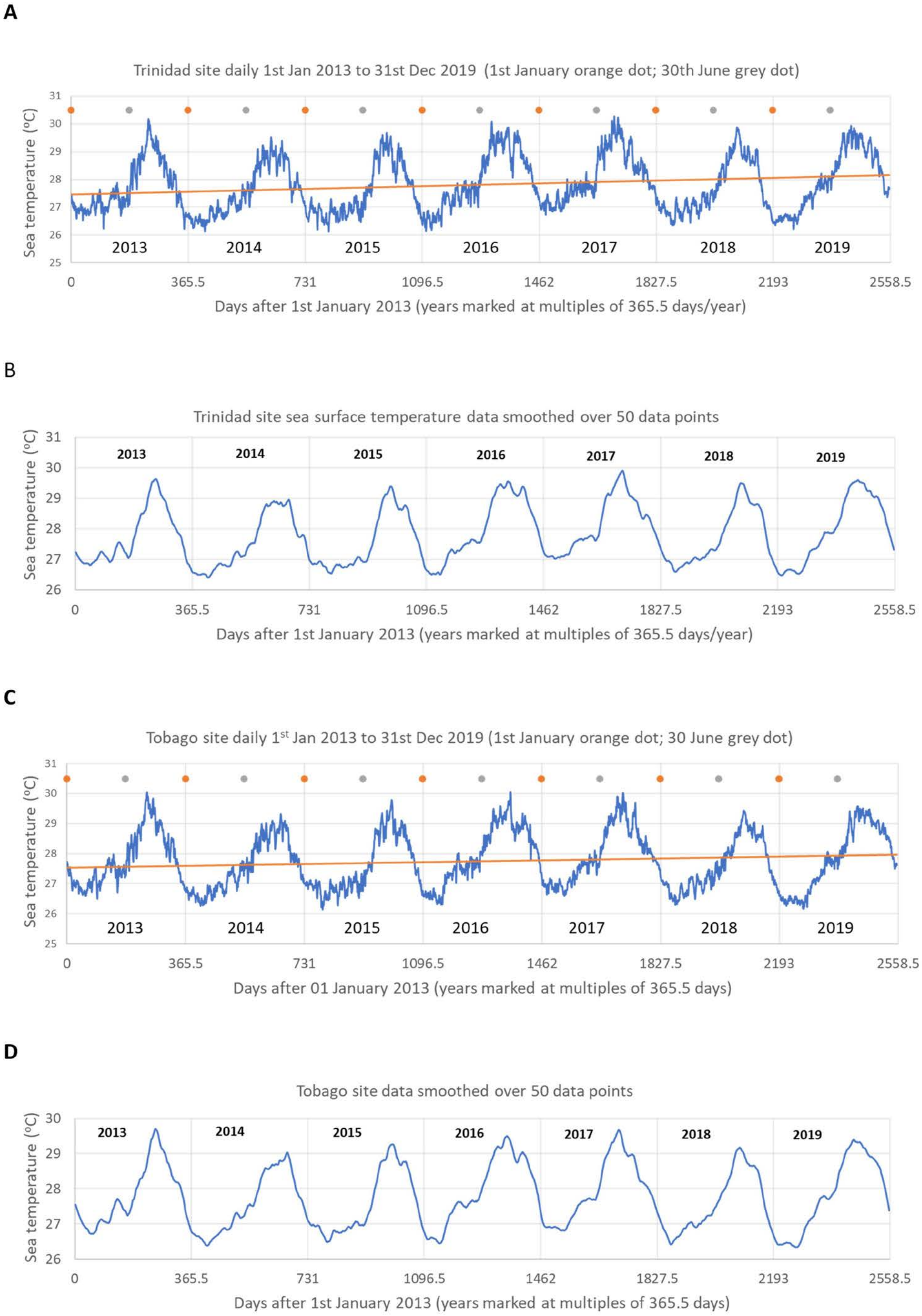


Figure 5. Daily sea surface temperatures measured offshore of the Trinidad and Tobago sites from 2013 to 2019. Sea surface temperatures were obtained from satellite data centred approximately 200 m offshore of each site. **A.** Daily records for the Trinidad sites as indicated for each year. The orange line is a simple regression line on all of the year data. **B.** The same data as in **A.** but smoothed over fifty data points using default smoothing procedure in ORIGINlab software. **C.** and **D.**, as for **A.** and **B.** above but for the Tobago site. Some of the smaller peaks (clearest in the smoothed data), appear to coincide with full moons and therefore consequent tidal changes. Note also the shoulders of warmer water appearing at both sites in 2016 and 2017 in the period before June 30th but not to nearly the same extent in the other years. Satellite-based sea surface temperature data cannot accurately indicate subsurface water temperatures, and are affected by factors such as evaporation, reflectance, waves and cloud cover.

Leatherbacks, for instance, may begin arriving in April at this site, meaning that the first half of the season occurs during the rising phase in sea temperatures covering as much as 3 °C. That part of 2016 and 2017 was unusual in that there was an early elevation in temperature that persisted for a while before rising rapidly to peaks achieved around the end of June.

DISCUSSION

We found year-to-year changes in the core body temperatures of two species of sea turtle with contrasting heat-conserving anatomies, physiologies and migratory patterns, nesting near-simultaneously in the same ocean area. If local sea temperatures, and thence turtle core temperatures, are pertinent to nest site selection, internesting periods and breeding phenology, then it may be useful to understand both the range of body temperatures and year-to-year fluctuations therein across different nesting areas as global ocean warming proceeds. The use of non-contact infrared thermometers, as used here, is effective for large-scale surveys that could readily detect trends.

Leatherbacks survive and forage in sea temperatures that would cause hypothermic incapacitation (cold-stun) in other species (James & Mrosovsky, 2004; James et al., 2005; 2006; Griffin et al., 2019). They achieve this resilience through extensive fat storage for thermal insulation, countercurrent vascular systems in their limbs and the muscles that operate them, and their sheer size ("gigantism") conferring a reduced surface area to volume ratio through which to lose heat (Frair et al., 1972; Greer et al., 1973; Davenport et al., 1990; Paladino et al., 1990; Davenport et al., 2015). Also, their constancy of swimming has been modelled to maintain an elevated body temperature (Bostrom & Jones, 2007; Bostrom et al., 2010). Cumulatively, these heat conservation features allow them to retain core body temperatures consistently above ambient sea levels (James & Mrosovsky, 2004; Patricio et al., 2021). The combination of these heat-conserving anatomy, physiology and behavioural features may result in them being better buffered against fluctuations in surrounding water temperatures than are hawksbills, as reflected in our findings.

Charting the SSTs adjacent to both of our nesting sites shows a close overall relationship (Fig. 4B), and regular annual cycles within which there was a gradual overall increase during our study period (Fig. 5). Surprisingly, therefore, the surface temperatures of the turtle eggs showed an overall slight decrease during the study years (Fig. 4C). This disparity could have been due to inconsistencies in how measurements were taken (though none such were apparent), or changes in the instruments used (though there were several infrared thermometers recruited over the years, all calibrated yearly). The incidental timings of our nocturnal field measurements could also have an effect on the overall trend seen; lunar cycles and tidal effects are known to affect the frequency of turtles coming ashore (Girondot et al., 2006) (lunar dates would, of course, change from year to year, tides presumably changing the temperature of near-shore waters). Also, in the years 2016 and 2017, warmer waters begin to appear before the summer peak earlier than in other years (Fig. 5). Nevertheless, the overall pattern of core temperature changes of both leatherbacks and hawksbills from year to year did approximately follow SSTs – the drops in June and July SSTs seen in 2015 and 2018 correspond to minima for both species of turtle core temperatures (Fig. 4C). Seeking body temperature versus sea temperature correlations may be confounded by satellite-based SST measurements being subject to error in indicating bulk subsurface temperatures due to evaporation, wind, wave action, infrared emissivity, reflectance and cloud cover (Barale et al., 2010). Possible inconsistencies aside, more interesting would be if changes in sea currents local to the study beaches were occurring, or that the turtles were changing where they were resting, mating or feeding before coming ashore.

Understanding how sea turtles may adapt their phenology of nesting in response to overall, or local ocean warming is important, especially given the changes that have already been observed (Neeman et al., 2015; Liles et al., 2019; Patricio et al., 2021; Laloe & Hays, 2023; Kirkham et al., 2025; Rickwood et al., 2025). Superficially, it would seem feasible for some species to exploit seasonal changes around a given rookery to move to more clement times – in our study area that could mean arriving to nest earlier in the year. This may be possible for hawksbills, but leatherbacks may be more limited in choice given the timing of their migration to and from the temperate waters where they feed on abundant Cnidarians prior to breeding (Holland et al., 1990; Davenport, 1998; Houghton et al., 2006; Doyle et al., 2007; Nordstrom et al., 2020). The other obvious change would be to move away from hot central tropical beaches. Sea turtles tend to return to their natal coastal areas to nest, but fidelity to particular beaches therein is not absolute (Nordmoe et al., 2004; Hamann et al., 2010). A degree of non-fidelity, behaviourally built-in or environmentally-induced, could be important to allow turtles to change nesting sites to improve their reproductive success. Any such changes that would trigger long-distance movements may take several generations, be affected by conditions on the foraging grounds, and energy stores that turtles can accumulate prior to migrating to nest.

There is increasing evidence that sea water temperatures by nesting sites can cause an adjustment of breeding phenology (when nesting seasons occur) and internesting periods (when females return to nest in the same season) in several species of sea turtle (Sato et al., 1998; Hays et al., 2002; Schofield et al., 2009; Weber et al., 2011; Colman et al., 2025; Fuentes-Tejada et al., 2025; Rickwood et al., 2025; Witt et al., 2025; Nugraha et al., 2026). Most of these studies used satellite-based SSTs, and some used data loggers attached, or connected internally to the animals. In the latter case, for instance, there are indications that the females sojourn in warmer zones of water before coming ashore (Schofield et al., 2009), and their temperatures can rise onshore (Sato et al., 1998). While clearly useful, single-point SSTs may not show up the complexity of water temperature zoning given the turbulent flow offshore. While measuring egg temperatures as proxies for core body temperatures, as here, may not solve this difficulty, it provides for simple-to-apply, large-scale surveys, that could go some way to understanding how female turtles select preferred temperatures before nesting – this would be particularly so for the smaller more ectothermic species.

Some recent studies have considered how vitellogenesis and embryogenesis will be influenced by female body temperatures and duration of internesting periods (Schofield et al., 2009; Marn et al., 2017), which will be particularly influential in ridley turtles between arribadas mass nesting events. While in our measurements we cannot know the order in which the emerging eggs were formed and embryogenesis began, it is clear that their temperatures are relatively uniform such that there is no apparent effect of differential proximity to a water-cooled surface or metabolically heated interior (Fig. 1). Thus, surveys need only measure a sample of the eggs released by a female, although this would need to be checked for other species.

There appears to be a degree of linkage between the Southern Oscillation (ENSO) of the eastern Pacific Ocean and conditions in the Atlantic Ocean (Enfield & Mayer, 1997; Gill et al., 2006; Chen et al., 2018; Hong et al., 2022; Cetina-Heredia & Allende-Arandía, 2023; Jiang et al., 2023; López-Pérez et al., 2024; Samset et al., 2024; Jury, 2025). Our observation period encompassed one strong El Niño year (the warm phase of the ENSO) between 2015 and 2016, two weaker El Niños, and two weak La Niña events (the cool phase of the ENSO), as indicated in Figure 3. There is insufficient information to discern any long-term patterns at this stage, or connection between ENSO and waters local to our observation sites, but it is noticeable that, for hawksbills, the strong 2015–2016 El Niño event was accompanied by an increase in core temperatures; the two following weak La Niñas with a reduction; and the two subsequent weak El Niños with slight increases, over a previous year.

While most attention is currently being paid to the consequences of changing temperatures of nesting beach sand and oceans for turtle reproduction in climate change, it may be that this could usefully be combined with observations on core body temperatures of the animals that may also influence their selection of breeding sites and phenology. This study illustrates that year-to-year variations are notable in the core body temperatures of nesting female sea turtles, here illustrated with two species that exhibit extremes in body size, extent of migrations and heat retention capacities. Such longitudinal surveys are straightforward to undertake and may ultimately contribute to understanding and predicting how sea turtles may, or may not, successfully alter their breeding sites and timings in the face of global climate change, and the challenges they may face before coming ashore.

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Data accessibility

All the data contributing to this study are in the main text and supplementary materials, or available from the author.

Ethical statement

The fieldwork at both the Trinidad and Tobago sites were carried out under permits issued by the Wildlife Section of the Trinidad and Tobago Government. No invasive or tissue sampling procedures were undertaken, the observations made did not disturb the animals' natural nesting and egg-laying processes, and there was no, or very minimal, contact with the animals, and always inadvertent.

Author contributions

Malcolm Kennedy planned the study, curated and analysed the data, administered the project, acquired the resources for field work equipment, created the figures, and wrote the paper. Please see Acknowledgements for appreciation of other people who contributed crucially to the work.

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