

Sand temperatures for nesting sea turtles in the Caribbean: Implications for hatchling sex ratios in the face of climate change



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ABSTRACT

A 200-year time series of incubation temperatures and primary sex ratios for green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) sea turtles nesting in St. Eustatius (North East Caribbean) was created by combining sand temperature measurements with historical and current environmental data and climate projections. Rainfall and spring tides were important because they cooled the sand and lowered incubation temperatures. Mean annual sand temperatures are currently 31.0 °C (SD = 1.6) at the nesting beach but show seasonality, with lower temperatures (29.1–29.6 °C) during January–March and warmer temperatures (31.9–33.3 °C) in June–August. Results suggest that all three species have had female-biased hatchling production for the past decades with less than 15.5%, 36.0%, and 23.7% males produced every year for greens, hawksbills and leatherbacks respectively since the late nineteenth century. Global warming will exacerbate this female-skew. For example, projections indicate that only 2.4% of green turtle hatchlings will be males by 2030, 1.0% by 2060, and 0.4% by 2090. On the other hand, future changes to nesting phenology have the potential to mitigate the extent of feminisation. In the absence of such phenological changes, management strategies to artificially lower incubation temperatures by shading nests or relocating nest clutches to deeper depths may be the only way to prevent the localised extinction of these turtle populations.

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1. Introduction

It is widely reported that climate change is having a profound impact on the functioning of ecosystems (Hoegh-Guldberg and Bruno, 2010). Species abundances and distributions are shifting due to the changing environment (Jones and Cheung, 2015; Poloczanska et al., 2013). The breeding phenology of migratory species is also changing in response to environmental change (e.g. McCarty, 2001; Parmesan et al., 1999; Walther, 2010). Furthermore, climate change-induced habitat loss puts species at risk of extinction when no alternative adequate habitat is available (Foden et al., 2013). The risk of climate change is particularly pronounced for marine ectotherms as they conform more closely to thermal tolerance limits than terrestrial ectotherms (Sunday et al., 2012) and, in particular, species whose biology and phenology are intimately linked to temperature (Somero, 2010). Of particular concern are species that exhibit temperature-dependent sex determination. This applies to the majority of reptiles, including sea turtles. The concern of climate change is of particular importance to sea turtles considering that six out of the seven species are classified as critically endangered,

endangered or vulnerable by the International Union for the Conservation of Nature (IUCN, 2014).

One of the conservation challenges for sea turtle ecologists is that climate change is impacting sea turtles in more than just one way. For instance, sea level rise may cause a loss of the beaches on which the females rely to nest (Fish et al., 2008; Fuentes et al., 2009a). Climate change models also predict an increase of rainfall and storm events at certain sites, which may be detrimental to nests as exposure to high levels of water negatively impacts the success of a nest (Patino-Martinez et al., 2014). Increasing air temperatures is also a concern for species that exhibit temperature-dependent sex determination and may lead to skewed sex ratios and local extinctions (Janzen, 1994). As such, increasing temperature was recently identified as one of the biggest threats to sea turtle populations' viabilities (Fuentes and Cinner, 2010).

Quantifying how warming temperatures will impact sea turtle populations across the globe is a conservation priority. A recent thread of research concerns the reconstruction of past sex ratios at important breeding sites based on historical air temperature data (e.g. Hays et al., 1999, 2003). These studies are important in informing how primary sex ratios fluctuated in the past. By using climate projections provided by the Intergovernmental Panel on Climate Change (IPCC) it is also possible to make projections on how the primary sex ratios may change in

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the future. This is of particular interest when trying to assess if a population is at risk of extinction in the near future due to climate change.

Current models used to estimate primary sex ratios are primarily based on air temperatures records alone (e.g. Hawkes et al., 2007; Hays et al., 1999, 2003). Such models are proven to be robust but having more variables may improve the model and make the reconstructions more accurate (Fuentes et al., 2009b). Working with the best available model is important when trying to accurately assess how global warming will affect the viability of sea turtle populations across the globe. The current study examines an array of environmental variables that may influence sand temperature of Zeelandia beach, St. Eustatius. Two hundred year time-series of incubation temperatures and primary sex ratios for the three species of turtles nesting at this site were then constructed. The results of this study inform on the extinction risks of these populations of sea turtles and help establish whether conservation efforts, such as shading or relocating nests, would be beneficial at this site.

2. Methods

2.1. Study site

The island of St. Eustatius (17.5°N, 63.0°W) is located in the Lesser Antilles in the North-eastern Caribbean (Fig. 1), with a land area of 21 km². Green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) turtles nest on St. Eustatius. The present study was conducted on Zeelandia beach (encompassing Turtle Beach to the South), a 1.6 km beach on the eastern, windward, exposed coastline of St. Eustatius where a monitoring programme of nesting turtles has been underway since 2002 (Debrot et al., 2005; Esteban et al., 2015).

2.2. Environmental variables

Historical rainfall data were obtained from the FD Roosevelt Airport on St. Eustatius (distance of 1.4 km from Zeelandia beach) from Weather Underground (www.wunderground.com/history/airport/TNCE, last

accessed on 12 August 2015). Daily precipitations were used to calculate monthly means.

Daily tide predictions for St. Barthélemy (distance of 43.4 km from St. Eustatius) were obtained from the National Ocean and Atmospheric Association (NOAA) (<http://tidesandcurrents.noaa.gov>, last accessed on 12 August 2015).

Air temperature and sea surface temperature data for the area between 16 and 18°N and 62–64°W were obtained from the International Comprehensive Ocean–Atmosphere Data (ICOADS) through the National Centre for Atmospheric Research (NCAR) (<http://rda.ucar.edu/datasets/ds540.1/>, last accessed on 22 May 2015). Data were downloaded at 2° spatial resolution from the Enhanced ICOADS Monthly Summary Release 2.5 and filtered to restrict the dataset to months with at least 20 observations. Data were not interpolated to fill in some gaps existing in the data set.

2.3. Air temperature projections

Air temperature projections were obtained from the United Nations Development Programme (UNDP). The projected values stem from an analysis of 15 climate models used by the IPCC for the fourth assessment report published in 2007 (www.geog.ox.ac.uk/research/climate/projects/undp-cp/, last accessed on 29 May 2015). The Special Report on Emissions Scenarios (SRES) scenario A2 was used for analysis. Projections that were published for the nation of St. Kitts and Nevis, two volcanic islands 12.4 km to the south-east of St. Eustatius, were used. The mean of the IPCC model output was bias-corrected using a “delta” approach: air temperature anomalies relative to the 1970–1999 mean air temperature in St. Kitts and Nevis were added to the 1970–1999 mean air temperature observed in St. Eustatius. To correct for variability, random variability was added based on the standard deviation of the historical ICOADS air temperature records to the model's output. 1000 runs were generated to capture the overall trend. The UNDP data is available in the form of yearly means and quarterly means. Quarterlies that encompass each turtle species' nesting season as recorded in 2002–2012 (JB, NE, STENAPA unpublished data) were used. For the hawksbills the yearly mean was used since this species nests from

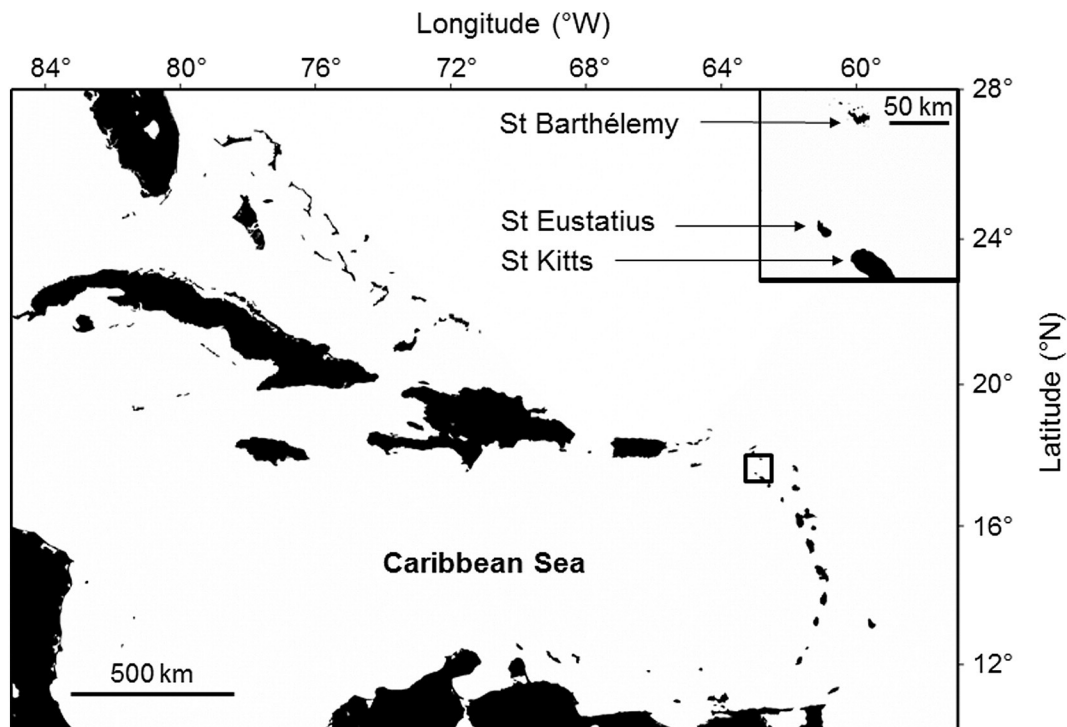


Fig. 1. Location of St. Eustatius in the Lesser Antilles in the north-eastern Caribbean. The study site, Zeelandia beach, is located on the eastern coast of St. Eustatius.

April until February. For the greens the quarterlies that span from March to November were used since the typical nesting season is from April until October. For the leatherbacks quarterlies that span from March through to August were used as nesting season is from February until July. These specific quarterlies were used during analysis both for the temperature reconstructions and temperature projections.

2.4. Sand temperature

Tinytag Plus 2 loggers (Tinytag Plus 2 models TGP-4017 and TGP-4500, Gemini Data Loggers, UK) were used to record sand temperature representative of nests for greens, hawksbills and leatherbacks nesting on Zeelandia beach during the 2011 and 2012 nesting seasons. Temperature measurements were recorded every hour. The loggers were originally calibrated to United Kingdom Accreditation Service (UKAS) standards and are accurate to <0.5 °C (www.tinytag.info, www.geog.ox.ac.uk/research/climate/projects/undp-cp, last accessed on 22 May 2015). To minimize impact on natural conditions during burial of loggers, care was taken to excavate a sand core and then replace it back on top of the logger. This was achieved by hammering a PVC pipe to the desired depth of the logger, creating a vacuum and then removing the pipe full of sand. The depth of the hole was verified using a semi-rigid tape measure, then the logger was dropped into the hole and the sand was emptied out of the pipe on top of the logger. A string was connected to the logger to facilitate relocation of loggers.

During the 2011 nesting season, eight permanent loggers were buried at locations along the beach, selected based on historical nesting activities: four at 44.6 cm depth (midpoint between 48.8 cm and 40.4 cm, the mean nest depths for greens and hawksbills respectively) and four at 63.3 cm (mean nest depth for leatherbacks). Mean depths were calculated from records as the midpoint between the top and bottom of clutches of eggs excavated between 2005–2010 (JB, NE, STENAPA, unpublished data).

During the 2012 nesting season, eight permanent loggers were buried at locations along the beach: four at 48.8 cm depth, mean nest depth for greens, and four at 63.3 cm, mean nest depth for leatherbacks (JB, NE, STENAPA unpublished data). Four additional loggers were deployed at 63.3 cm depth during March–June 2012. Two additional 'roving' loggers were re-positioned every seven days to record temperature conditions at the range of nest depths from 10 cm depth to 100 cm depth by 10 cm increments. Four complete cycles of 10 cm to 100 cm depth temperatures were recorded during the sample period. All roving loggers were buried on 17/02/2012 and excavated on 01/03/2013 to capture the first nesting activity and incubation period after the final nesting activity (Leatherback 24/04–17/06/2012; Green 29/05–14/11/2012; Hawksbill 17/02–26/12/2012).

2.5. Sand albedo

Albedo was measured to assess the relative reflection of the sand on Zeelandia beach and its relationship with sand temperature. Albedo measurements were taken with a standard photographic light metre (Sekonic L-778) following methods described in Hays et al. (2001) at the 12 permanent logger locations on Zeelandia beach. Albedo was calculated as the percentage of reflecting incident solar radiation from a surface:

$$\rho_{350-800} = (L_s / L_G) \times 18\%$$

where L_s is solar reflection of visible light from the sand, L_G is solar reflection of visible light from a grey card (of known albedo 18%) and $\rho_{350-800}$ is albedo (of the visible light). Albedo values were expressed as percentages (absorptance = 100% – albedo).

2.6. Primary sex ratios

The relationship between incubation temperature and primary sex ratios described in 2014 was used to calculate sex ratios (Laloë et al., 2014). A pivotal temperature of 29 °C was used as this temperature is illustrative for all species of sea turtles (Ackerman, 1997).

2.7. Hatchling emergence success

Year-round morning surveys (0600–0800 h local time) of Zeelandia beach have taken place since 2002 according to a standard protocol for nesting beaches (Eckert & Beggs, 2006). Any indication of turtle activity (i.e. tracks, sand disturbed in a way that was characteristic of nesting) was documented and the presence of eggs confirmed through careful digging by hand. Nightly beach patrols were conducted during peak nesting seasons from April–October (resources permitting).

Hatching success of recorded nests at Zeelandia beach was estimated from 2005–2010. Close to the expected hatching dates (after 50 days of incubation) the nest triangulation data were used to mark the site of the egg chamber. This area was closely monitored for evidence of hatching: a depression in the sand, hatchling tracks or hatchlings. When any signs of hatching were observed the nest was excavated after 48 h; if no signs of hatching were recorded the nest was excavated after at least 70 days from the date the eggs were laid. During an excavation, the nest contents were carefully removed from the egg chamber and inventoried. The data recorded for each excavated nest included the numbers of: empty shells (representing the number of hatched eggs), hatchlings, unhatched eggs (categorised as No Embryo, Embryo, Full Embryo), pipped eggs, predated eggs, deformed embryos, yolkless eggs; and depth of the top and the bottom of the egg chamber.

3. Results

3.1. Sand temperature and environmental variables

Five loggers were lost due to beach erosion or hurricanes. Loggers lost mid-season were replaced with new loggers. Data from the 15 loggers that were successfully retrieved were downloaded using Tinytag Explorer 4.7 and checked to ensure that logger time was synchronised with local time at the field site (GMT–4 h). Datasets were reviewed and data before logger deployment and after logger retrieval were removed. When processing the data monthly means were used. We excluded months for which days of data were missing from the analysis. Statistical analyses were performed using R (R Core Team, 2015).

Monitoring of sand temperature at mean green, hawksbill and leatherback turtle nest depths on Zeelandia beach during 2011–2013 provided 17 complete months of data from 15 permanent logger stations and a further 12 months of data from two roving loggers. Sand temperature tended to show seasonal variation, increasing during spring and summer towards a maximum in the months of July, August and September (Fig. 2) which coincided with peak nesting months of greens and hawksbills.

Rainfall and spring tides could be associated with temperature drops, either together or independently. Despite influencing sand temperatures, rainfall and spring tides were not good predictor variables for sand temperature.

3.2. Importance of depth

The results from the roving temperature loggers (depth range: 10–100 cm) helped understand the effect of depth on sand temperature at previously-recorded maximum nest depths for the study site. Sand temperatures at shallower depths were consistently higher than at deeper depths; the temperature range was highest during hotter months. Results for the roving temperature loggers at depths below mean nest depths showed a general pattern of warmer near-surface

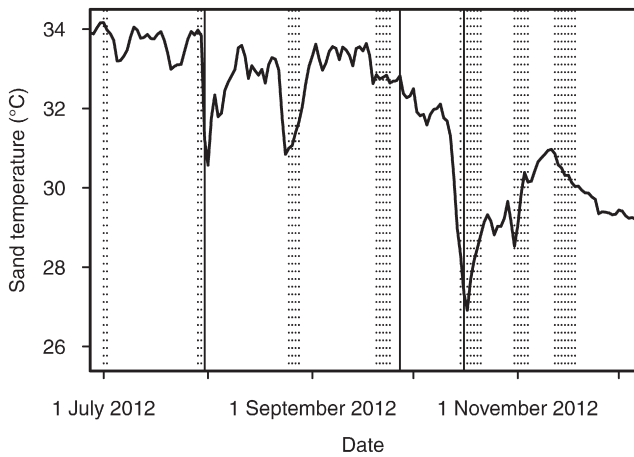


Fig. 2. Rainfall and spring tides have a short-term cooling effect on sand temperature in St. Eustatius. The vertical solid lines identify days for which daily precipitation is greater than 10 mm. The dotted lines identify days for which high tide predictions are greater than 50 cm (height above datum). Rainfall and spring tides can be associated with temperature drops, either together or independently, but not all cooling events are associated with one or the other.

sand temperatures and cooler temperatures at the maximum recorded nesting depth of 100 cm. For example, in April 2012 on Zeelandia beach, the temperature at 40–60 cm (the depth of the permanent loggers) averaged 30.5°C while the mean temperature at 100 cm was 1.0°C cooler. This general pattern occurred in different months although temperature did not always continue to decrease below 80 cm depth, perhaps due to the short term cooling effect of rainfall and spring tide on mean temperatures during some weeks (Fig. 3).

3.3. Sand albedo

On Zeelandia beach albedo $\rho_{350-800}$ was measured at the 12 permanent logger stations on 10 separate days between March–June 2012. The beach did not appear uniform in coloration: lighter areas appear in front of sandstone cliffs and darker areas near the rainwater gulleys. This impression was not supported by albedo measurements which revealed minor intra-beach variation ranging from 80.8% to 86.1% (mean

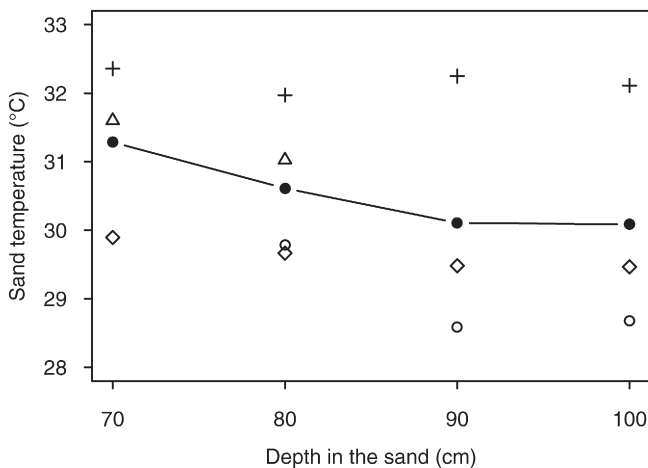


Fig. 3. General pattern of decreasing sand temperature with increasing depth. Each point represents the mean temperature for the duration that the logger was deployed at each depth: April (◇), June (+), August (△), and November (○). The studied months cover the incubation periods for leatherbacks (April, June), greens and hawksbills (June, August, November). The filled circles represent the mean for each depth. These depths correspond to the range of nesting depths at this site.

$\rho_{350-800}$ values; mean SD = 2.7%). The relationship between sand temperature at nest depths and the absorption of incident solar radiation by the sand was plotted, the results were not significant ($R = -0.02$, $p = 0.87$) therefore the effect of albedo of the sand of Zeelandia beach was excluded from subsequent analysis.

3.4. Incubation temperatures and primary sex ratios

A multiple stepwise regression reveals a strong relationship between air temperature and sand temperature (Multiple $R^2 = 0.60$, $F_{1,75} = 113.2$, $p < 0.001$) (Fig. 4). Addition of sea surface temperatures to the model only marginally improves the regression (Multiple $R^2 = 0.62$, $F_{2,74} = 60.11$, $p < 0.001$). An ANOVA comparing a model with sea surface temperatures to one without sea surface temperatures revealed that the models are not significantly different ($p = 0.07$) and so sea surface temperatures were not included in the model. Additionally, there was no significant effect of depth on sand temperature ($p = 0.84$) for the permanent (i.e. non-roving) loggers and so all loggers were pooled together. This lack of a depth cooling effect in the permanent loggers, most probably reflects that they were deployed over a much more restricted depth range than the roving loggers.

Using the relationship between air temperature and sand temperature (Fig. 4), sand temperatures since the late 1800s were reconstructed. A value of 0.5°C representing metabolic heating was then added to recreate incubation temperatures. This value is in line with values reported at nesting sites across the world (Howard et al., 2014). Fig. 5 shows the mean monthly incubation temperatures based on the ICOADS historical (1823–2014) air temperature data. Mean incubation temperature exceeded the pivotal temperature of 29°C during the entire nesting season duration so that the emerging hatchling population is predominantly female-skewed, with some seasonal variation due to the variance in mean temperature (Fig. 6a). Mean temperatures do not exceed thermal tolerance of 35°C (Ackerman, 1997) during the hottest period of the year and were used to predict sex ratios indicating an extremely high percentage of female clutches during the nesting season, from 40% female in February to >90% in June–November (Fig. 6b).

Projecting this model into the future, it is possible to estimate how incubation temperatures are likely to progress. It is estimated that mean incubation temperatures on Zeelandia beach will reach 32.1°C by the year 2030, 33.0°C by the year 2060, and 34.2°C by the year 2090 (Fig. 5).

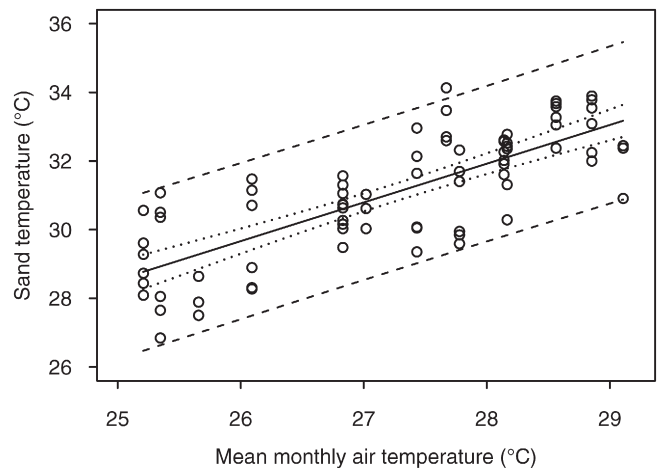


Fig. 4. Mean sand temperature (44.6–63.3 cm depth range) against mean (monthly) air temperature for St. Eustatius. A single point represents a monthly mean sand temperature recorded in 2011, 2012 or 2013. The solid line is the regression line, the dotted lines define the 95% confidence intervals, and the dashed lines define the 95% prediction intervals. The least squares fit regression equation is: mean sand temperature = $1.13 \times$ temperature + 0.33 ($R^2 = 0.60$).

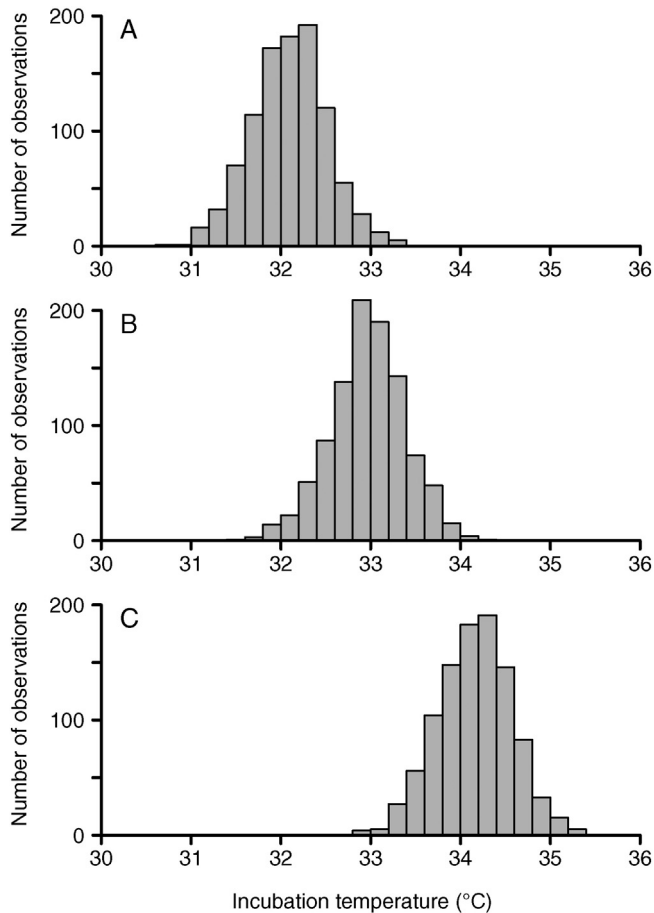


Fig. 5. Projection of incubation temperatures for Zeelandia beach. A projected increase of air temperatures at the study site will result in an increase of incubation temperatures. Predicted incubation temperatures were estimated for 1000 nests in 2030 (A), 2060 (B), and 2090 (C).

3.5. Primary sex ratios

Past sex ratios for Zeelandia beach were reconstructed using the relationship between incubation temperature and primary sex ratios described in 2014 (Laloë et al., 2014). No clear trend is visible for the reconstructed data with female production oscillating around 85.9–93.5% across species since the late 1800s (Fig. 7). Primary sex ratios have thus been historically female-biased for all three nesting species. When projecting into the future, warming air temperatures will exacerbate this female-bias: female sex ratios are projected to consistently reach >95% after the year 2045 for hawksbills and after 2028 for leatherbacks. It is likely that green turtle sex ratios have already been >95% since 2009.

3.6. Nesting surveys and hatching success

Results from surveys from an 11-year period (2002–2012) indicate a small nesting population on Zeelandia beach. Total nest numbers (probable and confirmed) were 255 (greens), 104 (hawksbills) and 100 (leatherbacks) for the 11-year period (JB, NE, STENAPA unpublished data). Emergence results were highly variable for greens ($42.5 \pm 38.3\%$, $n = 68$), hawksbills ($38.3 \pm 38.8\%$, $n = 17$) and leatherbacks ($11.3 \pm 19.4\%$, $n = 50$).

The incubation temperatures for all recorded nests were reconstructed to study the relationship between incubation temperature and emergence success (Fig. 8). There was no clear effect of temperature on emergence success. A large number of nests laid in the northern

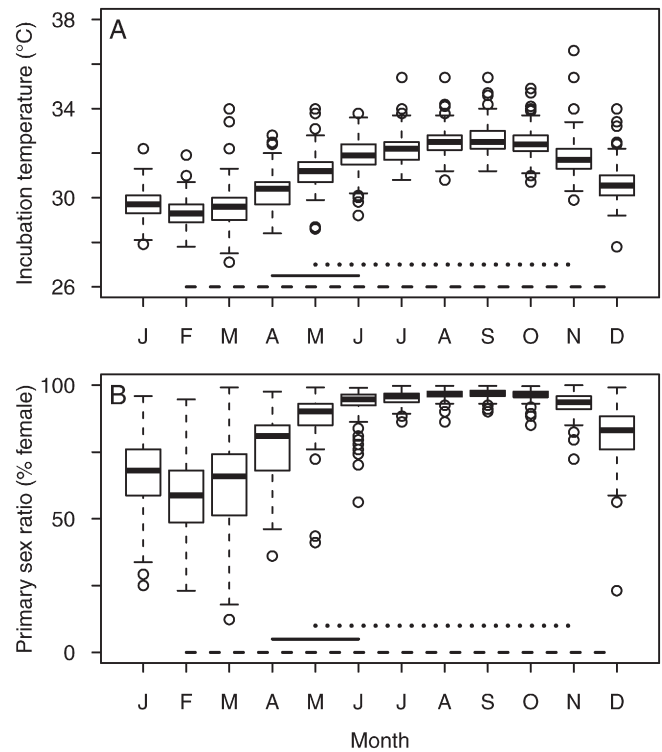


Fig. 6. (A) Seasonality of incubation temperatures at Zeelandia beach and (B) resulting sex ratios. Historical (1823–2014) air temperatures were used to reconstruct the mean monthly incubation temperatures across this 90-year period. The boxes delineate the upper and lower quartiles and the whiskers define the data's range. Outliers are plotted as separate points. The horizontal lines define the 2012 nesting seasons for each of the three turtle species nesting on St. Eustatius: greens (dotted line), hawksbills (dashed line), and leatherbacks (solid line).

sector of Zeelandia beach are close to a rainwater gully and several were found to be flooded during excavation (JB, NE, STENAPA unpublished data), possibly explaining the high number of nests with 0–40% emergence.

4. Discussion

Mean sand temperatures recorded at the study site were relatively high (29.1–33.3 °C) compared to other nesting beaches around the World. For example, mean sand temperatures at nest depths during nesting season were 29.0–31.0 °C in North Carolina, USA (De Gregorio and Southwood Williard, 2011), 29.5 and 32.2 °C for light and dark-coloured beaches respectively at Ascension Island (central Atlantic) (Godley et al., 2002); 30.3–32.4 °C in Barbados (Caribbean) (Horrocks and Scott, 1991); 29.5–33.2 °C in Greece (Mediterranean) (Godley et al., 2001); and 26.7–32.1 °C in Turkey (Kaska et al., 2006). There are few nesting beaches where sand temperatures are below 29 °C, including Queensland, Australia (Wood et al., 2014), southern Brazil (Baptistotte et al., 1999) and Huon Coast in Papua New Guinea (Steckenreuter et al., 2010). This finding of important differences in incubation temperatures around the World has also been made before (Hays et al., 2014) and implies that management plans to aid sea turtle conservation in a warming world need to be regionally tuned.

As in this study, female-biased primary sex ratios are being reported at other nesting grounds around the globe (e.g. Barbados, Caribbean; Cyprus, Mediterranean). At some sites female sex ratios as high as 100% are reported (Binckley et al., 1998; De Gregorio and Southwood Williard, 2011). Male-producing beaches still exist but seem to be the exception (Maulany et al., 2012; Steckenreuter et al., 2010; Stubbs et al., 2014). Our research at a female-biased turtle colony goes one step further by projecting how these sex ratios will progress in the

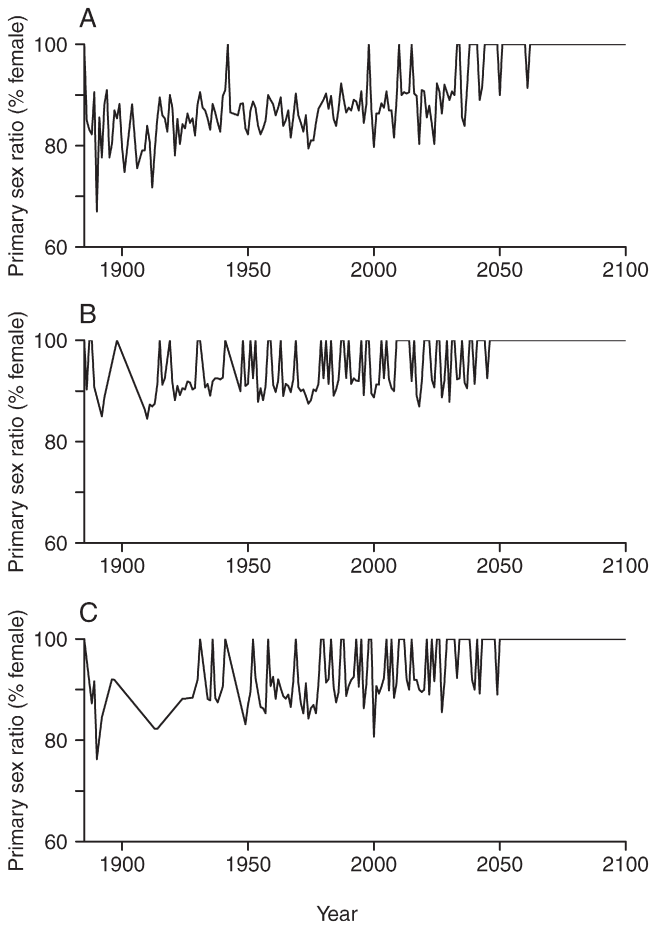


Fig. 7. Primary sex ratio reconstruction and projections. Female sex ratios were reconstructed and projected for green (A), hawksbill (B), and leatherback turtles (C). Each time-series takes into account the specific nesting season of each species, which explains the differences between time-series.

future. Results project the entire feminization of the three sea turtle populations in St. Eustatius due to increased air temperatures within the next century. Interestingly, results showed that all three populations have been historically strongly female-biased (Fig. 7) and this consistency across species supports the suggestion (Hays et al., 2014) that female hatchling skews may be adaptive. For example sea turtles are

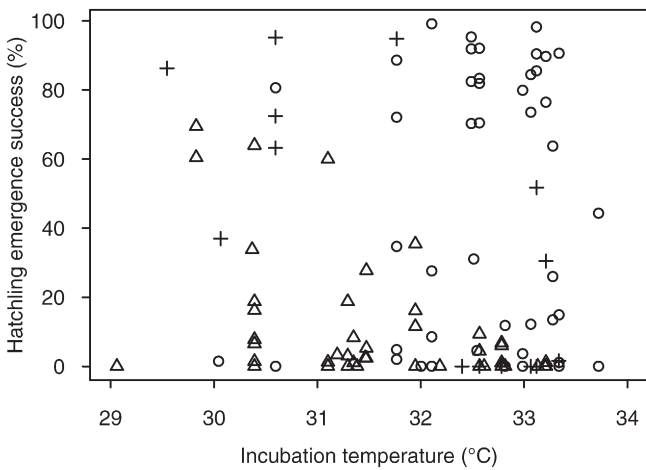


Fig. 8. Emergence success against incubation temperature. There is no clear effect of incubation temperature on emergence success for green (O), hawksbill (+), and leatherback turtles (Δ) at the study site. Most nests fall into two categories: >60% emerged or <40% emerged.

polygynandrous so a male will mate with more than one female during a breeding season. Additionally, females have the capacity to store sperm, which means that a female needs to mate with only one male to fertilise multiple clutches (Pearce and Avise, 2001). As such, an excess of females may be beneficial as it increases the number of clutches of eggs that can be laid in a season. Furthermore, males breed more frequently than females so that female-biased sex ratios translate to more balanced operational sex ratios (Hays et al., 2014). Taken together these findings suggest that female-biased primary sex ratios may be adaptive as they increase the population's natural growth rate (Laloë et al., 2014). In the long term, however, an extremely male-depleted population may not be viable. In this way, understanding how population dynamics are structured by primary sex ratios becomes an important conservation concern.

Despite considering a suite of environmental variables for the model, the most robust model put forth is one that only uses air temperature as a predictor variable for sand temperature. Sea surface temperatures were shown to be a good predictor of sand temperature in Northern Australia (Fuentes et al., 2009b) but addition of this variable to the model did not improve the output. On the other hand, similar relationships between air temperature and sand temperature were found at other sites across the world and were shown to be robust and informative (e.g. Hawkes et al., 2007; Laloë et al., 2014; Santidrián Tomillo et al., 2015). It was also shown that rainfall plays an important role in cooling sand temperatures, although it is not a useful predictor variable. This is likely due to the fact that rainfall events are inconstant throughout the nesting season and only have short-term cooling effects on sand temperatures.

It was already shown that protracted rainfall has a cooling effect on leatherback nests in Grenada and thus rainfall may allow for the production of more males in the Caribbean (Houghton et al., 2007). In addition to rainfall, this study demonstrates that tides with high coefficients are also important because they can affect the temperature of entire clutches of eggs. This may be the first time such a result has been reported in the literature. The implications of increased exposure of turtle nests to water (both from rainfall and spring tides) are two-sided: on one hand such events have the potential to cool nests and bring them both below the lethal thermal ranges for development and/or in the male producing thermal range. On the other hand, increased exposure to water can be detrimental to the incubating eggs as a strong negative correlation between sand water content and emergence success exists (Patino-Martinez et al., 2014). Furthermore, an excess of water above a nest can prevent gas exchanges between the air and the nest and asphyxiate the nest (Yalçın-Özdilek et al., 2007). This may be the variable causing a high mortality of nests at the study site. Recording rainfall and sea level rise thus become a conservation priority.

There are certain limitations to the model. For the purpose of succinctness the analysis focussed on scenario A2 in this article. This scenario is commonly used in studies (e.g. Christensen and Christensen, 2003; Wiens et al., 2009). If other SRES scenarios are considered, the overarching results and conclusions are likely to be the same but with varying degrees of urgency. As climate models are further reassessed and refined in the future, so will the ability to assess sea turtle population trends. There are also a suite of assumptions made in the model, including a pivotal temperature of 29 °C. Again, as more information about site-specific parameters are brought forward, the model can be further refined but, in the meantime, the general trends illustrated in the study are likely to hold true.

An important conservation concern is to assess whether or not species can adapt in the face of climate change. Results from this study hint towards potential phenological adaptation. The different turtle species at the study site are affected to varying degrees due to differences in breeding seasons (Fig. 6a). Hawksbill turtles have the lowest female sex ratios since these turtles nest ten months each year, during both warm and cool seasons. On the other hand, leatherbacks that nest during the warmest months of the year have the most female-biased sex

ratios of the three species. It is theoretically possible that by adjusting their nesting phenology with earlier or later nesting in cooler months, turtles would be able to maintain high female-biased sex ratios and low hatchling mortality rates. Nest depth may only play a limited role in controlling nest temperature at the current nesting depths. Yet since sand temperatures are cooler at extreme depths, if turtles are able to pick up on thermal cues of the sand and dig deeper nests, this would help produce viable nests even as the global temperatures warm. This is potentially an important research question to consider and merits more attention.

Not surprisingly, nest depth is coupled with female size (Horne et al., 2014) and reduced survivorship of clutches at shallower depths from smaller adult females may lead to an evolutionary shift towards larger turtles in future generations. Though, this may be obscured by the fact that higher incubation temperatures produce smaller turtle hatchlings (Burgess et al., 2006). In light of these results indicating the current feminisation of the turtle population and that temperature conditions will prohibit successful incubation of turtle nests at Zeelandia beach within 100 years, management practices at this site, and similar sites, may consider adaptations of nest relocation protocols. Adaptations may include relocation to deeper nests: for example, a nest at 100 cm depth is >1 °C cooler than the mean nest depth at Zeelandia beach; this depth is at the extreme end of the range of successful emergences from in situ nests as recorded at our study site. Another management strategy at some beaches is shading of surface sand by planting trees along the beach which may decrease temperatures as much as 1.8 °C (Wood et al., 2014).

The importance of modelling the effect of increased temperature on hatchling emergence successes is already suggested (Saba et al., 2012; Santidrián Tomillo et al., 2012, 2014, 2015). These studies show that warming temperature causes a reduction in female hatchling output due to decrease of hatching and emergence successes. Unfortunately the results presented in this paper regarding hatching success were inconclusive. Hatchling mortality in the face of climate change is an important question that warrants more attention. Until recently researchers focussed their efforts on understanding the relationship between incubation temperatures and sex ratios (Hawkes et al., 2009). Identifying the pivotal temperature for which both males and females are produced was a research priority (Howard et al., 2014) but now it is necessary to move beyond this and focus on the negative effects of high incubation temperatures, not limiting further research to the study of primary and operational sex ratios, but also to the study of hatchling mortalities. Only then will a holistic model assessing population viabilities be possible.

The results from this study underline the threats of climate change to sea turtle populations and highlight the extinction risks of climate change to species whose biology and phenology are closely linked to temperature. For sea turtles, increasing air temperatures has two effects: on one hand it will create female-biased sex ratios, and on the other hand it will increase temperature-linked hatching mortality.

This study demonstrates the need to study hatchling mortalities in relationship to increased incubation temperatures, highlights the importance of recording sand temperatures at varying depths, and demonstrates the usefulness of monitoring sand temperatures year-round to assess the potential that sea turtles have for phenological adaptations. Furthermore, investigation of mitigation measures to decrease incubation temperatures is recommended in order to increase survival of sea turtles at sites with high incubation temperatures.

Author contributions

NE and GCH conceived the study, NE led the fieldwork with assistance from JB, J-OL led the data analysis with contributions from all authors, all authors contributed to the writing. J-OL and NE are joint first authors.

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