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CLIMATE CHANGE AND SEA TURTLE NESTING

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Title/Author	**Impact of marine heatwaves for sea turtle nest temperatures / Hays, G. C., Chivers, W. J., Laloë, J. O., Sheppard, C., & Esteban, N.**
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Title/Author	**Influence of climate and tides on the nesting behaviour of sea turtles / Palomino-González, A., López-Martínez, S., & Rivas, M. L.**
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Title/Author	**The impacts of extreme El Niño events on sea turtle nesting populations / Santidrián Tomillo, P., Fonseca, L. G., Ward, M., Tankersley, N., Robinson, N. J., Orrego, C. M., Paladino, F. V., & Saba, V. S.**
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Adaptation of sea turtles to climate warming: Will phenological responses be sufficient to counteract changes in reproductive output?

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Abstract

Sea turtles are vulnerable to climate change since their reproductive output is influenced by incubating temperatures, with warmer temperatures causing lower hatching success and increased feminization of embryos. Their ability to cope with projected increases in ambient temperatures will depend on their capacity to adapt to shifts in climatic regimes. Here, we assessed the extent to which phenological shifts could

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M. M. P. B. Fuentes and J. R. Monsinjon contributed equally.

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mitigate impacts from increases in ambient temperatures (from 1.5 to 3°C in air temperatures and from 1.4 to 2.3°C in sea surface temperatures by 2100 at our sites) on four species of sea turtles, under a “middle of the road” scenario (SSP2-4.5). Sand temperatures at sea turtle nesting sites are projected to increase from 0.58 to 4.17°C by 2100 and expected shifts in nesting of 26–43 days earlier will not be sufficient to maintain current incubation temperatures at 7 (29%) of our sites, hatching success rates at 10 (42%) of our sites, with current trends in hatchling sex ratio being able to be maintained at half of the sites. We also calculated the phenological shifts that would be required (both backward for an earlier shift in nesting and forward for a later shift) to keep up with present-day incubation temperatures, hatching success rates, and sex ratios. The required shifts backward in nesting for incubation temperatures ranged from −20 to −191 days, whereas the required shifts forward ranged from +54 to +180 days. However, for half of the sites, no matter the shift the median incubation temperature will always be warmer than the 75th percentile of current ranges. Given that phenological shifts will not be able to ameliorate predicted changes in temperature, hatching success and sex ratio at most sites, turtles may need to use other adaptive responses and/or there is the need to enhance sea turtle resilience to climate warming.

KEYWORDS
adaptive response, climate change, ectotherms, marine turtles, phenology, reproductive output, sea turtles

1 | INTRODUCTION

The world's climate is changing at an unprecedented rate (Loarie et al., 2009). As a response, species, from polar terrestrial to tropical marine environments, have started to alter their phenology (e.g., timings of cyclical or seasonal biological events), shift their geographic distribution, and modify their trophic interactions (Dalleau et al., 2012; Parmesan & Yohe, 2003; Walther et al., 2002). Species' responses to climate change can occur through at least three contrasting but non-exclusive mechanisms: (1) range shifts, (2) phenotypic plasticity, and (3) microevolution via natural selection (Fuentes et al., 2020; Hulin et al., 2009; Waldvogel et al., 2020).

Range shifts might be observed by sea turtles responding to changes in climate by shifting their range to more climatically suitable areas (Abella Perez et al., 2016; Mainwaring et al., 2017). It is crucial that these areas provide the environment necessary for colonization and are conducive to egg incubation (Fuentes et al., 2020; Pike, 2013). However, it has been indicated that areas with climatically suitable environments might be impacted by other stressors (e.g., sea level rise, coastal development), which might hinder the potential adaptive capacity of sea turtles (Fuentes et al., 2020). Phenotypic plasticity allows individuals to cope with environmental changes and relates to the ability of individuals to respond by modifying their behavior, morphology, or physiology in response to an altered environment (Hughes, 2000; Hulin et al., 2009; Waldvogel et al., 2020). Microevolution refers to adaptation occurring because of genetic change in response to natural selection (Lane et al., 2018). Phenotypic plasticity provides the potential for organisms to respond rapidly and effectively to environmental changes and thereby cope with short-term environmental change (Charmantier et al., 2008; Przybylo et al., 2000; Réale et al., 2003). However, phenotypic plasticity alone may not be sufficient to offset against projected impacts from climate change (Gienapp et al., 2008; Schwanz & Janzen, 2008). Microevolution, on the other hand, is thought essential for the persistence of populations faced with long-term directional changes in the environment. However, the ability of microevolutionary responses to counteract the impacts of climate change is unknown, because rates of climate change could outpace potential responses (Hulin et al., 2009; Morgan et al., 2020; Visser, 2008) although see Tedeschi et al. (2015).

It is unclear whether potential adaptive responses by turtles will be sufficient to counteract projected impacts from climate change (Monsinjon, Lopez-Mendilaharsu, et al., 2019; Moran & Alexander, 2014; Morjan, 2003). For example, sea turtles have persisted through large changes in climate during the millions of years that they have existed, demonstrating a biological capacity to adapt (Maurer et al., 2021; Mitchell & Janzen, 2010; Rage, 1998). Nevertheless, there is growing concern over the potential impacts that projected temperature increases might have on sea turtles (Patrício et al., 2021). Temperature plays a central role in sea turtle embryonic development, hatching success, hatchling sex ratios (Hays et al., 2017; Standora & Spotila, 1985), hatchling morphology, energy stores, and locomotor performance (Booth, 2017). Sea turtle eggs only successfully incubate within a narrow thermal range (25 and ~35°C), with incubation above the thermal threshold resulting in hatchlings with higher morphological abnormalities and lower hatching success (Howard et al., 2014; Miller, 1985). Furthermore, sea turtles have temperature-dependent sex determination, a process by which the incubation temperature determines the sex of hatchlings (Mrosovsky, 1980). The pivotal temperature (PT ~28.9–30.2°C for the species studied here, Figure S1), where a 1:1 sex ratio is produced, is centered within a transitional range of temperatures (~1.6–5°C, Figure S1), that generally produces mixed sex ratios. Values above the PT will produce mainly female hatchlings while values below produce mainly males (Mrosovsky, 1980).

Thus, projected increases in temperature may cause feminization of sea turtle populations and decrease reproductive success (Patrício et al., 2021). Many studies have suggested that sea turtles may adapt to increases in temperature by altering their nesting behavior, through changes in their nesting distribution, and nest-site choice (Kamel & Mrosovsky, 2006; Morjan, 2003), and by shifting nesting to cooler months (Almpanidou et al., 2018; Dalleau et al., 2012; Pike et al., 2006; Weishampel et al., 2004). Earlier nesting has already occurred in some turtle populations as a response to climatic warming (e.g., Pike et al., 2006; Weishampel et al., 2004). However, it is unclear whether phenological and behavioral shifts can sufficiently buffer the effects of rising temperatures (Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon, Lopez-Mendilaharsu, et al., 2019). Although two other studies (Almpanidou et al., 2018; Laloë & Hays, 2023) have explored whether earlier shifts in phenology can preserve the present-day thermal niche of sea turtle nesting environment in a changing climate, only one other study (Monsinjon, Lopez-Mendilaharsu, et al., 2019) explores the implications of phenological responses to sea turtle reproductive output (hatching success and primary sex ratio), of which they focused on loggerhead turtles (*Caretta caretta*). Given that different sea turtle species have different spatial–temporal nesting patterns, we expand from this study focused on loggerhead turtles to assess the extent to which phenological shifts by four different species of sea turtles could mitigate increases in temperature at different sea turtle nesting sites globally to maintain the reproductive output of affected populations. Furthermore, to build on previous work, we explore whether nesting populations could benefit from both an earlier and a later phenological shift. To do so, we calculated the shift (backward and forward, respectively) that would be required for incubation temperature, hatching success, and sex ratio to stay similar to current ranges. In doing so we are the first study to date to investigate the implications of a later nesting by sea turtles.

2 | MATERIALS AND METHODS

2.1 | Modeling framework

We considered the capacity of green (*Chelonia mydas*, *Cm*), loggerhead (*Caretta caretta*, *Cc*), hawksbill (*Eretmochelys imbricata*, *Ei*), and olive ridley (*Lepidochelys olivacea*, *Lo*) turtles to counteract the impacts of climate change on incubation temperature, hatching success, and sex ratio by temporally shifting their nesting season. We included 24 nesting sites globally which are part of 11 different regional management units (RMUs as per Wallace et al., 2010; Table S1). To predict overall hatching success and sex ratios at our study sites (scaling up spatially and temporally across levels: from the nest to the whole rookery; across the entire nesting period), we followed a method developed by Monsinjon, Wyneken, et al. (2019) for the loggerhead sea turtle (Figure 1). We calculated a seasonal indicator of mean incubation temperature (average weighted by the number of nests), hatching success (average survival proportion weighted by the number of nests), and sex ratio (average male or female proportion weighted by the hatching success and the number of nests). The approach consisted of six steps: (1) reconstruction of current (1979–2020) nest temperature at nesting sites, (2) modeling embryonic growth in clutches from the same RMU, (3) inferring thermal tolerances at the species level, (4) developing sex ratio thermal reaction norms at the species level, (5) describing nesting seasonality for each nesting site, and (6) forecasting nest temperature, hatching success and sex ratio under a scenario of climate warming, while considering a potential temperature-driven shift in nesting phenology (Figure 1). We give details on each step below and highlight any adjustments or improvements applied in the present study in relation to the Monsinjon, Wyneken, et al. (2019) analysis.

2.2 | Current clutch temperature

Based on a correlative approach with sea surface temperature and air temperature (Bentley et al., 2020; Fuentes et al., 2009; Girondot & Kaska, 2015; Laloë et al., 2020; Monsinjon, Jribi, et al., 2017), we reconstructed the daily nest temperature at each of our study sites between January 1979 and December 2020. For this, we obtained sea and air temperatures from the European Centre for Medium-Range Weather Forecasts (ECMWF) climate reanalysis v5 (ERA5; hourly time series at 0.25° × 0.25° spatial resolution; Hersbach et al., 2020) at each site and fitted a linear mixed-effect model to our in situ daily nest temperatures using the R package "nlme" (Pinheiro et al., 2022) with nest identity as random effect and an ARMA correlation structure. To estimate metabolic heating (i.e., the increase in temperature within the egg chamber as compared to the surrounding incubation substratum), we used the proportion of incubation time as an additional predictor. This produces a proxy for metabolic heating specific to each nesting site (Monsinjon, Guillon, et al. (2017) for details). The values obtained (i.e., the increase in temperature at the end of incubation, Table S1) ranged from 0.46 to 5.55°C, which is similar to those presented by

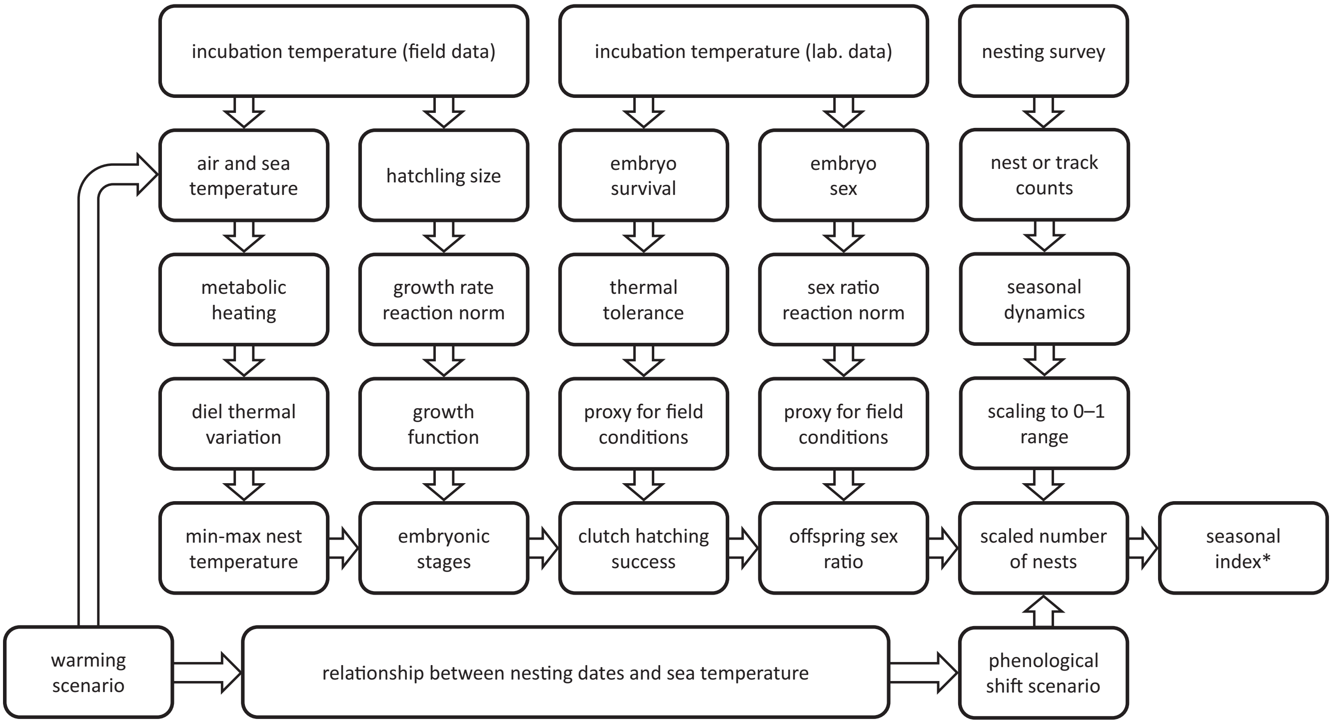

FIGURE 1 Modeling framework to predict overall hatching success and sex ratio at our study sites (scaling up from the day-nest level to the season-beach level), modified from Monsinjon, Wyneken, et al. (2019). * is to indicate seasonal index of incubtaion temperature, hatching success or sex ratio.

(Gammon et al., 2020). Based on the lowest Akaike information criterion (Burnham & Anderson, 2002), we selected the best model from a set of candidates using a daily lag with air or sea temperature varying from 0 (i.e., synchronous relationship with nest temperature) to 5 days (i.e., lagged relationship with nest temperature at day+5). Following (Monsinjon, Guillon, et al., 2017), we used the standard deviation of the coefficients of the random effect as a proxy of nest thermal heterogeneity at the nesting beach scale (see Monsinjon, Wyneken, et al., 2019) for its application in sea turtles. Finally, we estimated the coefficients of each predictor (sea surface temperature, air temperature, and proportion of incubation time) for the selected model within a standard generalized linear model framework using a Gaussian link function. To reconstruct diel thermal fluctuation, we computed daily maximum and minimum temperatures as follows: average daily temperature ± average daily amplitude (as defined by daily maxima − daily minima). We set daily maximum and minimum temperatures at the average time of day (decimal hours) when they occurred (mean daily amplitude and average time of day for minima and maxima are given in Table S1 along with the other parameters used to reconstruct nest temperatures).

2.3 | Embryonic development

To predict the progression of embryo size during incubation and hence estimate the dates of each embryonic stage along our nest temperature time series, we used two equations describing, respectively, the thermal reaction norm of embryonic growth rate and a growth function of incubation time (Fuentes et al., 2017; Girondot et al., 2018; Girondot & Kaska, 2014; Monsinjon, Jribi, et al., 2017) using the R package "embryogrowth" (Girondot, 2022a). This method requires nest temperature data and measurements of the straight carapace length of hatchlings. Based on our field data (Table S1) and assuming a Gompertz model for embryo growth, we estimated the four parameters of the model (Schoolfield et al., 1981) using maximum likelihood (Girondot & Kaska, 2014). Here we identified the posterior distributions to compute confidence intervals using Bayesian Markov chain Monte Carlo (MCMC) with the Metropolis–Hasting algorithm (Chib & Greenberg, 1995) on 10,000 iterations. We used the values estimated with maximum likelihood as initial parameters and assumed a uniform distribution for priors. To ensure the acceptance rate across iterations was optimal, we followed the adaptive proposal distribution procedure (Rosenthal, 2011) implemented in the R package "HelpersMG" (Girondot, 2022b). Once calibrated, we ran the embryonic growth model along reconstructed nest temperatures to estimate, for any given day a clutch would be laid, the duration of incubation (i.e., when embryo size reaches hatchling size) and the position of the thermosensitive period of development for sex determination within that nest (Girondot et al., 2018).

2.4 | Thermal tolerance and hatching success

We used the flexible-logistic model described in Abreu-Grobois et al. (2020) and implemented in the R package "embryogrowth"

(Girondot, 2022a) to describe the transition from maximal to 0% survival at temperatures where embryos fail to develop. This model allows for asymmetrical transitions in survival proportion at lethal temperatures (i.e., around 25°C and 33–35°C, with variation among species, Howard et al., 2014). We estimated the parameters of the thermal tolerance curve specifically for each species using literature data on hatching success measured at several controlled temperatures (i.e., held constant) during incubation experiments (Table S2). We first estimated the parameters using maximum likelihood and then we identified the posterior distributions to compute confidence intervals following the procedure described above (i.e., Bayesian MCMC with the Metropolis–Hasting algorithm and the adaptive proposal distribution) on 100,000 iterations assuming a uniform distribution for priors. Following Monsinjon, Wyneken, et al. (2019) and Laloë et al. (2020), we calculated hatching success from the mean temperature during the whole incubation after applying a correction parameter to control for deviations unrelated to temperature (Monsinjon, Wyneken, et al., 2019). The correction parameter was estimated by comparing in situ hatching success data (using data from the literature and the present study: see Table S3) with predicted ones (i.e., from mean temperature + correction factor) and searching for the value that minimizes the dispersion of residuals. As previous studies used +0.32°C for loggerhead turtles (Monsinjon, Wyneken, et al., 2019) and +0.82°C for green turtles (Laloë et al., 2020), we restricted our search between −1°C and +1°C.

2.5 | Sex ratio thermal reaction norm

To predict sex ratio (i.e., the proportion of males or females) at the scale of a clutch, we estimated the thermal reaction norm of sex ratio (i.e., the relationship between male proportion and temperature when held constant during incubation) using the logistic equation described in Monsinjon et al. (2022) and implemented in the R package "embryogrowth" (Girondot, 2022a). We estimated the equation parameters specifically for each species using literature data on sex ratio measured at several controlled temperatures (i.e., held constant) during incubation experiments (Table S4). We first estimated the parameters using maximum likelihood and then identified the posterior distribution of the parameters using Bayesian MCMC with the Metropolis–Hasting algorithm and the adaptive proposal distribution on 100,000 iterations assuming a Gaussian distribution for priors. We used a Gaussian distribution here since the values for the parameters do not vary much among sea turtle species. From our embryonic growth model, we estimated the position of the thermosensitive period of development (BeginTSP to EndTSP in the equation below), using the values estimated by Monsinjon et al. (2022) for sex determination during incubation and extracted temperature traces and increments of embryo size within this period (Girondot et al., 2018). As pointed out in previous research (Fuentes et al., 2017; Georges et al., 1994, 2005), the simple mean temperature is not an appropriate proxy for sex ratio. Therefore, we calculated a growth-weighted average temperature (i.e., a constant temperature equivalent or CTE) and, following a recent improvement (Monsinjon et al., 2022), we added the level of sexualization (initially estimated for loggerhead turtles nesting in Florida, USA) to the weighting scheme. We calculated the growth-weighted sexualization-weighted average temperature (CTE) as follows:

$$\text{CTE} = \frac{\sum_{t=\text{BeginTSP}}^{\text{EndTSP}} \left(T_t \times \Delta\text{time} \times \text{Growth} \times \text{TRNS}\left(T_t\right) \times \text{S} - \text{TSP}(t)\right)}{\sum_{t=\text{BeginTSP}}^{\text{EndTSP}} \left(\Delta\text{time} \times \text{Growth} \times \text{TRNS}\left(T_t\right) \times \text{S} - \text{TSP}(t)\right)},$$

where T_t is the temperature at time t, Δtime is the time difference between two successive records, Growth is the size increment between two successive records, and $\text{TRNS}\left(T_t\right) \times \text{S} - \text{TSP}(t)$ is the level of sexualization defined by the thermal reaction norm of sexualization (TRNS) at T_t and the sensitivity of sexualization during the TSP (S – TSP) at time t.

2.6 | Nesting dynamics

To scale up incubation temperatures, hatching successes, and sex ratios at the scale of a clutch to the whole nesting season based on daily nest numbers, we estimated the overall nesting dynamics (i.e., the progression of nest number throughout any season) at our study sites (see Figure S2). To do this, we used the model described in Girondot (2010, 2017) available in the R package "phenology" (Girondot, 2020). This model uses a negative-binomial distribution for each ordinal day and has seven parameters that define nesting seasonality: (1) the date of the peak of nesting, (2) the average number of nests (or tracks) at the peak of the season, (3) its duration, (4) the minimum number of nests (or tracks) in periods out of the nesting season, (5) the duration from the beginning of the season to the peak and (6) from the peak to the end (the beginning and the end being estimated via the parameter 4), and (7) a negative-binomial parameter that controls for the dispersion around the mean. These parameters are components of a model described in Girondot (2010, 2017). This model uses all available nests (or tracks) to estimate the date of the beginning and the end of nesting seasons (via the parameters 1, 5, and 6, described above), which is more appropriate than using the first and the last nesting attempts that could be sporadic events not representative of the underlying nesting dynamics (e.g., if nesting occurs all year round). Here, we assumed that the maximum did not flatten out around the peak, which is consistent with the bell-shaped distribution of nest count data typically observed at our study sites. To minimize constraints on the parameters that control for the shape of nesting seasonality (i.e., when nesting begins, peaks, and ends), we estimated the maximum of each nesting season first while holding the "shape" parameters constant. Then we fixed the maximum to its estimated value, and we estimated the "shape" parameters in a second round. Finally, we standardized the overall nesting dynamics (number of nests or tracks per day) between 0 and 1 so that all nesting sites are treated the same way, assuming a constant nesting success throughout the season. We treated the site Tetiaroa Atoll (French Polynesia) with a different set of equations (described in Laloë et al., 2020) derived from the aforementioned model (Girondot, 2010, 2017) because green turtles can attempt to nest on each of the 12 islets (see Laloë et al., 2020) which are not monitored with the same effort. Given the varying nesting proportion and monitoring effort at this site we estimated the maximum for each islet and each season to determine the overall nesting dynamics of this site. For computation efficiency purposes, we assumed the minimum number of nests was always zero during the low season, except for olive ridleys nesting at Las Cabras (Mexico). In this case, we also estimated season-specific minima because a non-negligible number of turtles came to nest sporadically all year round. We first estimated the parameters using maximum likelihood and then their distribution was estimated using Bayesian MCMC with the Metropolis–Hasting algorithm and the adaptive proposal distribution on 10,000 iterations assuming a Gaussian distribution for priors.

2.7 | Climate and phenology scenarios

We considered two climate scenarios: current (hindcasting between 2007 and 2020) and the IPCC's SSP2-4.5 "Middle of the road" scenario (IPCC, 2021); forecasting between 2059 and 2100. We predicted incubation temperature, hatching success, and sex ratio within the last two decades to stay representative of current day conditions and chose from 2007 onward as this period contains >97.5% of our hatching success field data (Table S5). We extracted mean temperature and sea surface temperature anomalies from the web interface (https://interactive-atlas.ipcc.ch/regional-information) of the IPCC's Atlas (Gutiérrez et al., 2021) with the following settings: Region set = WGI reference-regions (or Small islands for the Tetiaroa Atoll, French Polynesia), Uncertainty = Advanced, Season = Annual, Baseline period = 1981–2010, and Future period = 2081–2100. For both variables and within each region, we extracted the median change in temperature (Table S1). To forecast daily minimum and maximum nest temperatures between 2059 and 2100, we added those anomalies to our 1979–2020 baseline time series of air and sea surface temperature and applied the model calibrated on contemporary data. We then computed daily hatching success and sex ratio along forecasted nest temperatures by iterating the steps described earlier. Finally, we considered three plausible phenology scenarios: (1) no shift in nesting phenology, or (2) nesting dates will shift either 6.86 days earlier (hereafter referred to as the "mean" shift, ±SD = 4.23, $n = 16$; Table S6) or (3) 18.85 days earlier (hereafter referred to as the "maximum" shift, found in Mazaris et al., 2008) for every 1°C rise in sea surface temperature at nesting sites. We calculated the mean and maximum shifts based on an extensive search of previous studies that reported a significant negative relationship between nesting dates and seawater temperature in sea turtles (Table S6). We did not consider non-significant or positive relationships between the proxy for nesting phenology and the environmental cue (i.e., a delay of nesting dates with increasing temperatures instead of a shift earlier as assumed in the present study). Based on these relationships and the expected regional anomalies in sea surface temperature under the SSP2-4.5 warming scenario, we estimated the expected number of days shifted in the future at our study sites (Table S1) and forecast our seasonal indicators of incubation temperature, hatching success, and sex ratio accordingly. When considering if sites would remain within current rates we considered conditions within a 2.5% of the present-day values for hatching success and sex ratio shift (i.e., difference between 25th percentile of current and median of future <2.5% reduction) and within 0.5°C buffer for incubating temperature (i.e., difference between median of future and 75th percentile of current <0.5°C). To complement this analysis, we also calculated earlier and later phenological shifts that would be required in the future to stay within current conditions. To do so, we shifted nesting seasons backward (from −1 to −365 days) and forward (from +1 to +365 days) and we retained the minimum number of days earlier or later when the following conditions are met for each indicator: (1) median incubation temperature index ≤75th percentile of current indices, (2) median hatching success index ≥25th of current indices, and (3) median sex ratio (male proportion) index ≥25th percentile of current indices.

2.8 | Sensitivity analysis and fit quality

As sufficient data were not available specifically for each RMU, we fitted thermal tolerance curves and sex ratio thermal reaction norms at the species level (i.e., pooling all available data, individually for each species) to benefit from the existent extensive literature data (Tables S2 and S4). This approach allowed us to predict hatching success and sex ratio for sites where data were unavailable or too scarce at the RMU level (i.e., lack of data at low or high temperatures, Table S1). For our sensitivity analysis, we compared our predicted hatching success and sex ratio seasonal indices using either species-wide or RMU-wide data when available for both hatching success and sex ratio laboratory data. This allowed us to compare the outputs for loggerheads from the "Atlantic, Northwest" RMU (2/6 loggerhead sites; 1/4 RMUs), hawksbills from the "Atlantic, Western Caribbean/USA" RMU (4/7 hawksbill sites; 1/4 RMUs), and olive ridleys from the "Pacific, East" RMU (2/3 olive ridley sites; 1/2 RMUs), but we could not compare the outputs for green turtles (eight green turtle sites; five RMUs) because there were no data available for any of the RMUs (thermal tolerance curves and sex ratio thermal reaction norms are presented in Figure S1 and details on sites and RMUs can be found in Table S1). We evaluated the robustness of our predictions by comparing predicted daily mean nest temperatures with recorded ones. We calculated the R^2 coefficient of determination as a measure of fit quality.

3 | RESULTS

Under a "middle of the road" warming scenario (SSP2-4.5), the air temperature will increase on average by 1.5–3°C, and local sea surface temperature will increase by 1.4–2.3°C by 2100 across our study sites, resulting in a 0.58–4.17°C increase in sand temperatures (Table S1). According to the maximum expected phenological shift (18.85 days earlier for every 1°C rise in local sea surface temperature), nesting seasons could shift from 26 to 43 days earlier on average by 2100 at our study sites ($n = 24$, Table S1).

Currently (2007–2020), the median incubation temperature at our study sites is 30.1°C (25th–75th percentiles = 29.1–30.8°C), ranging from 26.1 to 32.1°C (*Cc* 26.1–32.1°C, *Cm* 28.8–32.1°C, *Ei* 28.5–31.6°C, *Lo* 30.3–30.7°C; Figure 2; Figure S3). Under a "middle of the road" scenario (2059–2100), the median incubation temperature will rise to 31.7°C (25th–75th = 30.7–32.8°C), ranging from 28 to 35.7°C (*Cc* 28–35.7°C, *Cm* 29.9–34.4°C, *Ei* 30.3–33.7°C, *Lo* 32.3–33.1°C). With a maximum expected shift in phenology, the median decreases to 31°C (25th–75th = 30.1–32.5°C), ranging from 26.6 to 34.2°C (*Cc* 26.6–33.9°C, *Cm* 29.7–33.6°C, *Ei* 28.8–33.8°C, *Lo* 31.9–34.2°C; Figure 2). With a maximum shift in phenology only seven sites would be able to maintain current incubation temperature or lower. To keep up with present-day incubation temperature the required shifts backward, for an earlier nesting, ranged from −20 to −191 days (Figure S3; Table S7), whereas the required shifts forward, for a later nesting, ranged from +54 to +180 days. To note for half of the sites no matter the shift the median temperature will always be warmer than the 75th percentile of current ranges. The relationship between nesting dates and SSTs (i.e., the phenological rates) that would allow the required phenological shifts to be achieved are presented in Table S7.

Currently, the median hatching success rate at our study sites is 80.1% (25th–75th = 74.3%–82.7%), ranging from 53.5% to 84.5% (*Cc* 76.1%–84.5%, *Cm* 73.2%–82.6%, *Ei* 65.7%–84%, *Lo* 53.5%–68.9%; Figure 3; Figure S4). Under a "middle of the road" scenario, hatching success rates will drop to 67.4% (25th–75th = 46.3%–78.2%), ranging from 1% to 84.5% (*Cc* 1%–84.5%, *Cm* 50.4%–81%, *Ei* 42.6%–75.2%, *Lo* 26.5%–57.5%), and with the maximum expected shift in phenology hatching success rates increases to 69.1% (25th–75th = 50.8%–79.9%), ranging from 15.3% to 84.5% (*Cc* 27.5%–84.5%, *Cm* 59.1%–81.3%, *Ei* 41.1%–83.1%, *Lo* 15.3%–58.2%), with 10 of the 24 nesting sites being able to maintain similar hatching success rates to current values (Figure S4; Table S8). To keep current hatching success rates, the required shifts backward for an earlier nesting ranged from −1 to −172 days (Figure S4; Table S7), whereas the required shifts forward for a later nesting ranged from +1 to +252 days. With half of the sites being unable to maintain current hatching success rates no matter the shift undertaken. The relationship between nesting dates and SSTs (i.e., the phenological rates) that would allow the required phenological shifts to be achieved is presented in Table S7.

Currently 6 of the 24 nesting sites produce more than 90% of female hatchlings and 6 of the 24 sites produce at least 50% male hatchlings (Figure 4; Figure S5). We predicted that under a "middle of the road" scenario, 16 of the 24 nesting sites will produce clutches comprising more than 90% female hatchlings, with only one site (*Lepidochelys olivacea* in las Cabras, Mexico) producing clutches with more than 50% male hatchlings. However, with the maximum expected phenological shifts, the number of sites producing more than 90% of females will reduce to 11, and three sites would produce more than 50% of males. Overall, with the maximum expected phenological shift, half of the sites will be able to maintain current sex ratios (Figure S5; Table S8) of which seven are expected to produce more than 25% males (loggerheads in Wassaw Island and Dalyan Turtle beach, greens in Akyatan and Alagadi Turtle beaches, hawksbills in Fuwairit, and olive ridleys in Rushikulya and Las Cabras). The required shifts backward to keep current male proportions ranged from −1 to −149 days (Figure S5; Table S7), whereas the required shifts forward ranged from +1 to +160 days. With eight sites being unable to keep current sex ratio no matter the shift undertaken. The relationship between nesting dates and SSTs (i.e., the phenological rates) that would allow the required phenological shifts to be achieved is presented in Table S7.

3.1 | Model robustness

Overall, there is good agreement between predicted and recorded daily incubation temperatures with a R^2 of .71 (Figure 5) that ranges from .2 to .91 when temperatures are compared individually for each site (Figure S6). Our sensitivity analysis shows that seasonal indicators of hatching success can be different for hawksbills (i.e., hatching success always higher under the warming scenario considered here when using data at the species level) when using either species-wide or RMU-wide laboratory data to adjust the model for thermal tolerances (Figure S7). On the other hand, we did not detect substantial differences for loggerheads and olive ridleys, for both indicators of hatching success and sex ratio.

4 | DISCUSSION

The maximum expected shift in nesting phenology will allow for some sites to maintain similar incubation temperatures ($n = 7$), hatching success ($n = 10$), and sex ratio ($n = 12$) to current values (2007–2020). However, for half of the sites no matter the shift in phenology current rates of incubation temperature and hatching success will not be able to be maintained, with eight sites being unable to keep current male production no matter the shift undertaken. These results align with similar studies which found variability in the ability of phenological shifts to maintain current temperature levels and consequently productivity (Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon, Wyneken, et al., 2019), with nesting sites further from the equator (>30° latitude) showing to have the greatest capacity to buffer impacts of predicted increases in nest temperatures (this study and Laloë & Hays, 2023). The inability for nesting phenology to counteract predicted changes in temperature and productivity is of concern.

Several studies, including this one, have predicted a reduction in hatchling production as temperatures increase, which would impact population growth and stability (Laloë et al., 2017; Montero et al., 2019; Montero, Ceriani, et al., 2018; Santidrián Tomillo

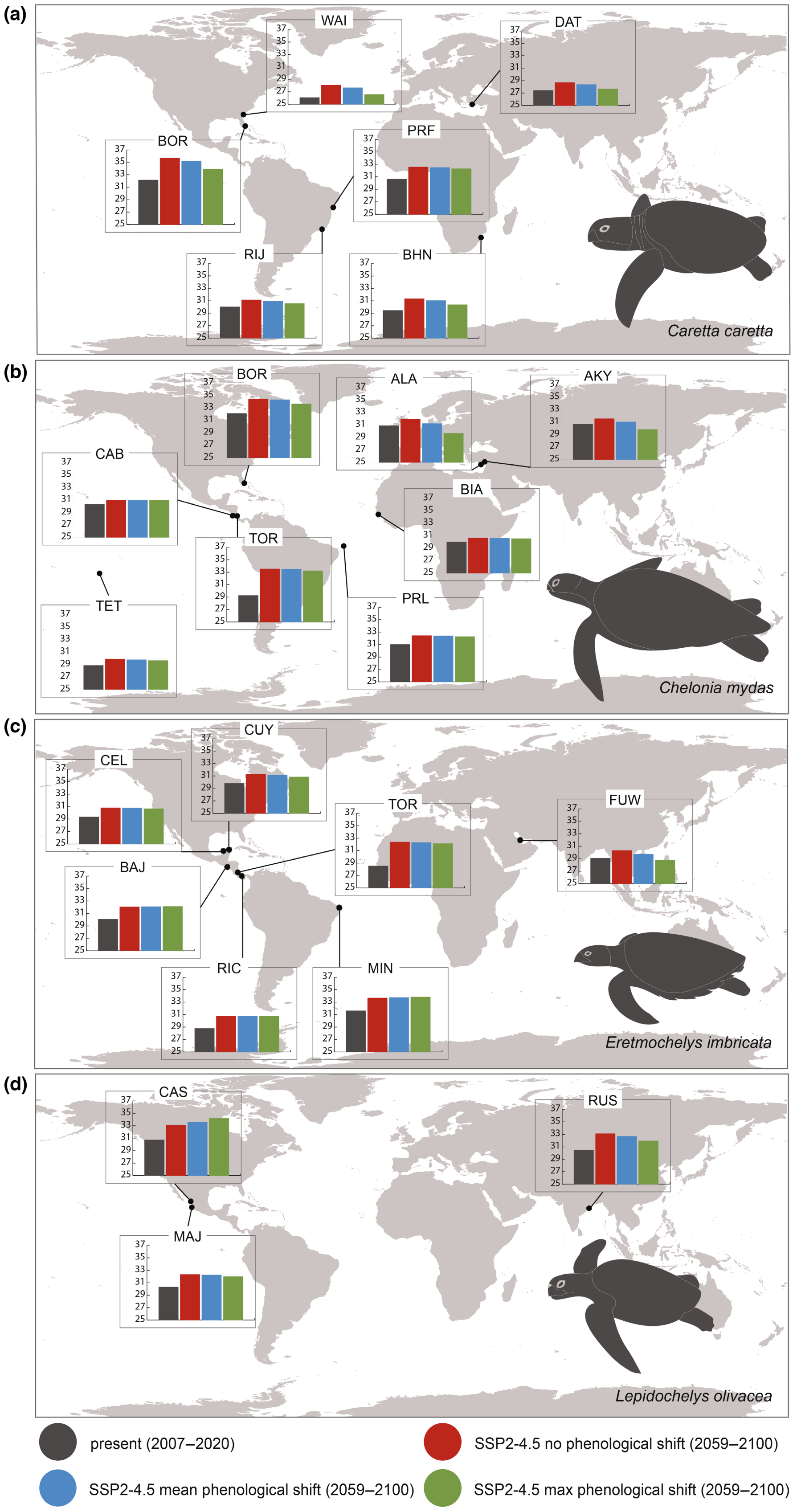

FIGURE 2 Current (2007–2020) absolute mean incubation temperature, and future (2059–2100) incubation temperature across the whole incubation period under a middle of the road scenario (SSP5-48.5) with and without an earlier phenological shift (26–43 days) for (a) loggerhead turtles (*Caretta caretta*), (b) green turtles (*Chelonia mydas*), (c) hawksbill turtles (*Eretmochelys imbricata*), (d) olive ridley (*Lepidochelys olivacea*). AKY, Akyatan beach, Türkiye; ALA, Alagadi Beach, Cyprus; BAJ, Bahía de Jiquilisco, El Salvador; BHN, Bhanga Nek, South Africa; BIA, Bijagós Archipelago, Guinea-Bissau; BOR, Boca Raton, Florida, USA; CAB, Cabuyal, Costa Rica; CAS, Las Cabras, Mexico; CEL, Celestún, Mexico; CUY, El Cuyo, Mexico; DAT, Dalyan Turtle Beach, Türkiye; FUW, Fuwairit, Qatar; MAJ, Majahuas, Mexico; MIN, Minas, Brazil; PRF, Praia do Forte, Brazil; PRL, Praia do Leão, Brazil; RIC, Rio Caña, Panama; RIJ, Rio de Janeiro, Brazil; RUS, Rushikulya, India; TET, Tetiaroa, France; TOR, Tortuguero, Costa Rica; WAI, Wassaw Island, USA.

et al., 2015). Furthermore, even though sea turtle populations are typically female bias (Hays et al., 2014), greater production of female hatchlings in relation to current rates (median female proportion across our study sites between 2007 and 2020 ≈ 70%) may ultimately result in unbalanced sex ratios of breeding adults (Schwanz et al., 2010), which might alter reproductive dynamics, reducing

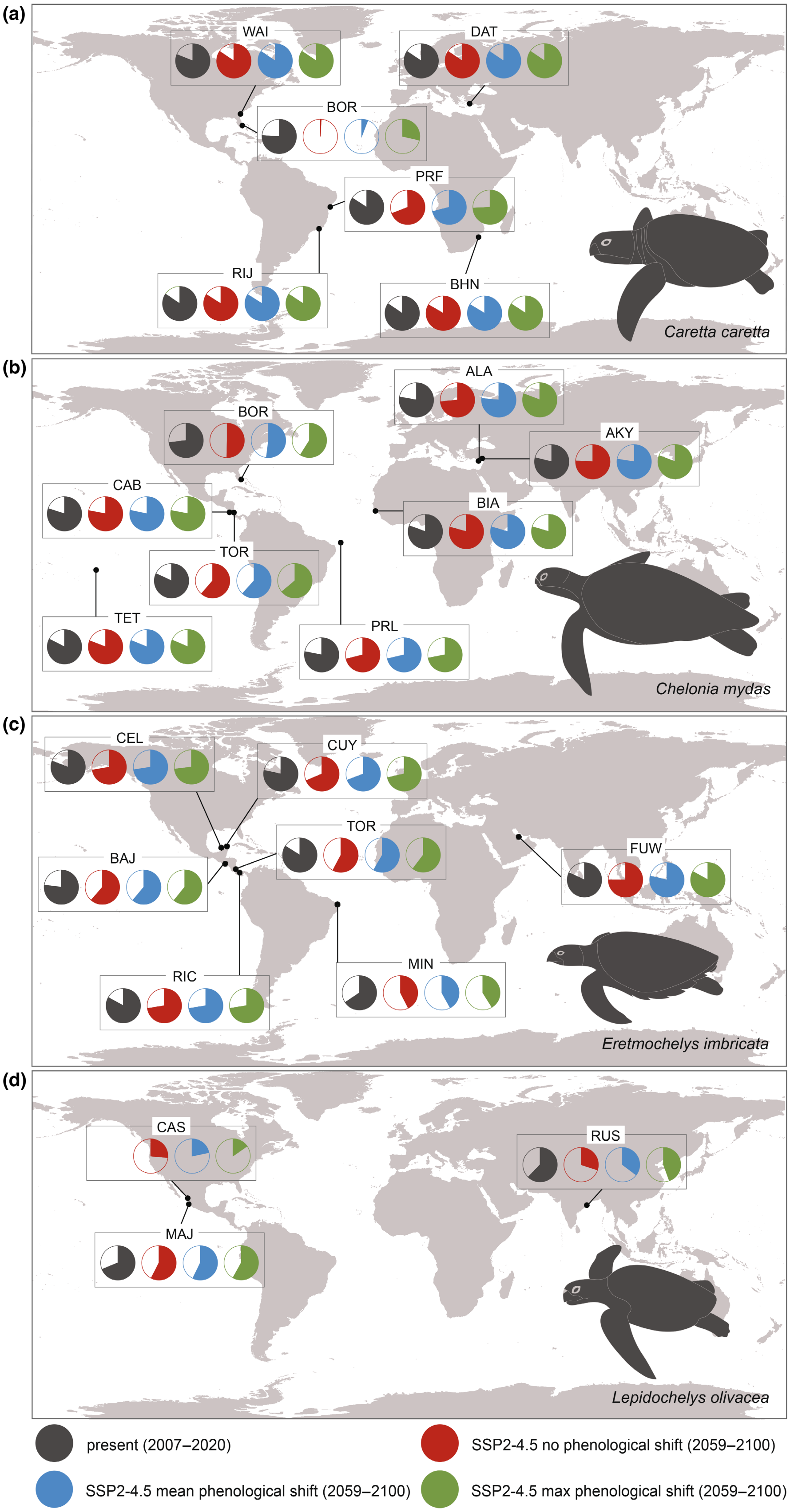

FIGURE 3 Current (2007–2020), and future (2059–2100) hatching success projections under a middle of the road scenario (SSP2-4.5) with and without an earlier phenological shift (26–43 days) for (a) loggerhead turtles (*Caretta caretta*), (b) green turtles (*Chelonia mydas*), (c) hawksbill turtles (*Eretmochelys imbricata*), and (d) olive ridley (*Lepidochelys olivacea*). Full charts indicating 100% hatching success AKY, Akyatan beach, Türkiye; ALA, Alagadi Beach, Cyprus; BAJ, Bahía de Jiquilisco, El Salvador; BHN, Bhanga Nek, South Africa; BIA, Bijagós Archipelago, Guinea-Bissau; BOR, Boca Raton, Florida, USA; CAB, Cabuyal, Costa Rica; CAS, Las Cabras, Mexico; CEL, Celestún, Mexico; CUY, El Cuyo, Mexico; DAT, Dalyan Turtle Beach, Türkiye; FUW, Fuwairit, Qatar; MAJ, Majahuas, Mexico; MIN, Minas, Brazil; PRF, Praia do Forte, Brazil; PRL, Praia do Leão, Brazil; RIC, Rio Caña, Panama; RIJ, Rio de Janeiro, Brazil; RUS, Rushikulya, India; TET, Tetiaroa, France; TOR, Tortuguero, Costa Rica; WAI, Wassaw Island, USA.

the incidence of multiple paternity and fertilization rates, as well as resulting in loss of genetic variation (Booth et al., 2021; Fuller et al., 2013; Hays et al., 2023; Manning et al., 2015). Feminization of populations may lead to demographic collapses (Mitchell & Janzen, 2010), although some evidence suggests that a shorter period between breeding bouts in males and promiscuous breeding

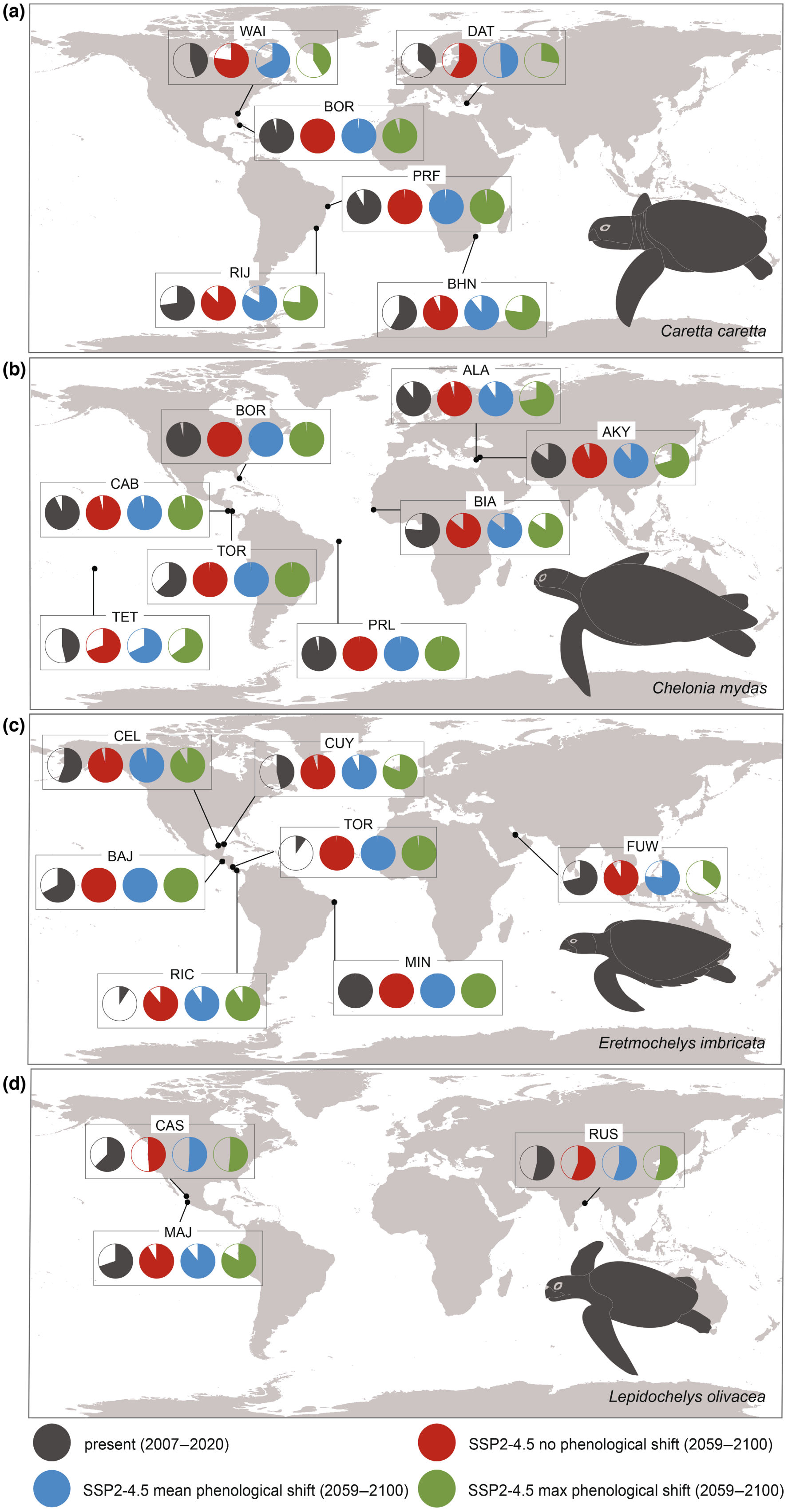

FIGURE 4 Current (2007–2020), and future (2059–2100) projections of female hatching production under a middle of the road scenario (SSP2-4.5) with and without an earlier phenological shift (26–43 days) for (a) loggerhead turtles (*Caretta caretta*), (b) green turtles (*Chelonia mydas*), (c) hawksbill turtles (*Eretmochelys imbricata*), and (d) olive ridley (*Lepidochelys olivacea*). Full charts indicate 100% female production. AKY, Akyatan beach, Türkiye; ALA, Alagadi Beach, Cyprus; BAJ, Bahía de Jiquilisco, El Salvador; BHN, Bhanga Nek, South Africa; BIA, Bijagós Archipelago, Guinea-Bissau; BOR, Boca Raton, Florida, USA; CAB, Cabuyal, Costa Rica; CAS, Las Cabras, Mexico; CEL, Celestún, Mexico; CUY, El Cuyo, Mexico; DAT, Dalyan Turtle Beach, Türkiye; FUW, Fuwairit, Qatar; MAJ, Majahuas, Mexico; MIN, Minas, Brazil; PRF, Praia do Forte, Brazil; PRL, Praia do Leão, Brazil; RIC, Rio Caña, Panama; RIJ, Rio de Janeiro, Brazil; RUS, Rushikulya, India; TET, Tetiaroa, France; TOR, Tortuguero, Costa Rica; WAI, Wassaw Island, USA. To note estimation is not directly obtained from Figure 2, but rather derived from temperatures during the TSP.

behavior may help balance operational sex ratios in warmer climates (Hays et al., 2023). The long-term consequences of skewed primary and adult sex ratios on population dynamics and the proportion of males required to sustain populations need to be fully understood for more robust assessments of the impacts of climate change on sea turtles (Boyle et al., 2014, 2016; Heppell et al., 2022). Similarly,

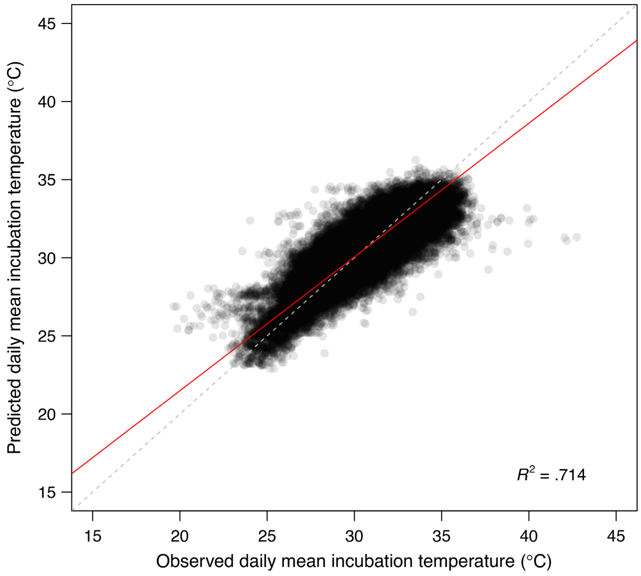

FIGURE 5 Predicted versus observed daily mean incubation temperatures (all study sites pooled together). The gray dashed line is the line of equality, and the red line shows the orthogonal regression.

for studies that aim to predict future hatchling production, such as this one, lack of data on the relationship between constant temperatures and hatching success remains problematic as well as lack of knowledge of how to integrate varying temperatures into constant equivalent temperatures and a lack of understanding on metabolic heating and its contribution to hatching success (Gammon et al., 2020, 2021). Such data gaps hindered our ability to include leatherback (*Dermochelys coriacea*) and flatback (*Natator depressus*) turtles in our assessment. For these species, we lack hatching success data below lower and above upper lethal temperatures (i.e., ~25 and ~35°C, respectively, Howard et al., 2014) to properly estimate thermal tolerance limits from laboratory experiments although see Gammon et al. (2021).

It is also important to consider that our study focuses on temperature-driven hatching success whereas other environmental factors, such as precipitation and moisture have also been found to influence hatching success (Montero, Marcovaldi, et al., 2018; Rafferty et al., 2017). For instance, embryos can die from suffocation if the nest is flooded from heavy rainfall for an extended period or from desiccation in the opposite case. Moreover, precipitation can cause incubation temperatures to drop via direct cooling or evaporation (Lolavar & Wyneken, 2021; Tezak et al., 2018), which has resulted in the suggestion that nest watering could potentially be used as management strategy to reduce heat-induced egg/hatchling mortality and to manipulate hatchling sex ratios (e.g., Gatto et al., 2023; Hill et al., 2015; Jourdan & Fuentes, 2015; Smith et al., 2021). However, human-assisted cooling of nests comes with a series of costs and benefits. Costs include the persistent need of human resources if temperatures continue to increase and a potential slowdown of natural selection via the retention of deleterious alleles. Benefits include a demographical boost if rescued embryos make it to adulthood and reproduce as well as the maintenance of appropriate genetic mixing if primary sex ratios translate into an optimal balance between reproductive males and females (Patrício et al., 2021). Nevertheless, if managers decide to manipulate the incubation of eggs, it is crucial to evaluate the consequences and define a strategy that requires the least human resources. Based on controlled incubation experiments, Porter et al. (2021) mimicked the effect of heavy rainfall by dropping incubation temperatures for 3 or 7 days during the thermosensitive period for sex determination (TSP). For eggs incubating at constant, female-producing temperatures, the results suggest that short temperature drops below the pivotal temperature can be sufficient to trigger the development of males and that the sensitivity to these drops throughout the TSP varies between green and loggerhead turtles. As discussed by the authors, this can be useful to target when to cool down the nests in natural conditions. A potential research avenue would be to refine the results presented in Patrício et al. (2021) by determining what would be the smallest drop in both temperature difference and duration sufficient to reach a specific proportion of males at any given temperature throughout incubation.

Our sensitivity analysis suggests that hatching success predictions for hawksbill turtles can differ when using data at the RMU level when compared to the species level, especially under the “middle of the road” (SSP2-4.5) warming scenario (Figure S7). This likely reflects a lack of data at the RMU level for this species. Although we did not detect substantial differences for olive ridley and loggerhead turtles, it is recommended to use hatching success and sex ratio data at the RMU level to account for local adaptation (or maladaptation) in thermal tolerances and pivotal temperatures. We encourage further research to obtain such data to refine the results presented here and extend our assessment of adaptive capacity to other sites and species. Furthermore, other limitations must also be taken into consideration when interpreting our results. First, we forecast future incubation temperatures based on a correlative model (i.e., via generalized linear models) whereas a mechanistic one (i.e., based on thermodynamics and biophysics principles) would be more appropriate (Bentley et al., 2020). We found an overall good agreement between incubation temperature predictions and observations, except for some sites for which high temperatures are largely underestimated (Figure S6). This is problematic when projecting warming impacts as we might underestimate exposure to female-producing and lethal temperatures. On the other hand, a mechanistic microclimate model (e.g., NicheMapR; Kearney & Porter, 2017) requires extensive information on sand physical properties, beach topography, vegetation, and local weather, which makes it difficult to apply extensively and globally (Fuentes & Porter, 2013). Second, we projected hatching success solely based on temperature, but future studies must integrate the combined effect of other climatic variables such as temperature and humidity, and consider uncertainties related to climate-driven changes in these variables. Third, we predicted clutch sex ratios using a recent, more sophisticated approach, namely the thermal reaction norm for sexualization (Monsinjon et al., 2022). However, this method requires extensive data on hatchling sex ratios under fluctuating temperature regimes and thus was applied so far only for loggerhead turtles nesting in Florida. Further research must be undertaken to investigate potential variations among species and populations in the timing of the TSP and the sensitivity of sexualization. Finally, we assumed that earlier phenological shifts are driven by temperature at nesting sites, in which case turtles would be waiting for optimal conditions for nesting after their arrival, with higher temperatures speeding up egg maturation (Monsinjon, Lopez-Mendilaharsu, et al., 2019; Pike, 2009; Schofield et al., 2009). However, sea turtle nesting phenology is yet to be fully understood as other studies suggest that the environmental cue turtles respond to might be sensed before their departure from foraging areas (Mazaris et al., 2009; Monsinjon, Lopez-Mendilaharsu, et al., 2019). We did not investigate this because the location of foraging areas connected to our nesting sites was unknown for most of the sites considered here. In addition, it is sometimes unclear whether other factors are involved (e.g., demography) in observed phenological shifts (Monsinjon, Lopez-Mendilaharsu, et al., 2019; Robinson et al., 2014), which makes it difficult to disentangle the effect of temperature. We encourage further studies to finetune the calculation of expected phenological shifts, specifically for each nesting population, by considering multiple factors (e.g., temperature, demography, migratory connectivity, and foraging habitat productivity).

Even though some work is still necessary to improve the spatiotemporal scale of our results, and that some improvements can be potentially made with our modeling approach our study provides another step toward a multi-species evaluation of climate change impacts on sea turtles' embryonic stage and sets the baseline for future research on this topic. For example, even though we only considered the influence of temperature on hatchling success, our results allow us to identify which sites might be more vulnerable/resilient to changes in temperature and that will suffer from warming-related shortage of hatchlings (i.e., the sites potentially at risk from rising temperatures only), which is particularly relevant for ectothermic species like sea turtles. Ultimately, the broad geographic span of our study sites, and consideration of four of the seven species of sea turtles, indicate that the impacts of climate change and the ability of phenological shifts to counteract potential feminization of sea turtles and decreases in hatching success will vary spatially and among species with some populations being unable to take advantage of phenological shifts, as previously indicated by similar studies (see Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon, Wyneken, et al., 2019). Having said this, we identified five sites (Wassaw Island, USA, Daylan beach, and Akyatan beach in turkey, Alagadi Beach in Cyprus and Fuwairit, Qatar) in which a maximum phenological shift will result in more males being produced than currently without a reduction in hatching success as observed at Las Cabras, Mexico. Ultimately, the impact of climate change on sea turtles and their resilience to it will depend on several factors such as population size, genetic diversity, non-climate-related threats, foraging plasticity, the availability of climatically suitable habitat, and their capacity to adapt (Fuentes et al., 2013, 2020; Patrício et al., 2021). Here, we only considered the ability of sea turtles to adapt through shifts in nesting phenology, which alone will likely not be sufficient to counteract the projected impacts of climate change on sea turtle reproduction (Almpanidou et al., 2018; Monsinjon, Wyneken, et al., 2019). It might be that several other processes need to take place for sea turtles to be able to adapt to climate change. Other behavioral adaptations may include changes in the spatial distribution of sea turtle nesting sites, as well as changes in their nest-site choice on nesting beaches (Cardona et al., 2022; Girard et al., 2021; Hochscheid et al., 2022; Mancino et al., 2022; Tomillo et al., 2022). Since spatial and temporal adaptations may occur simultaneously (Chuine, 2010), future studies should develop a multi-faceted framework to explore the adaptive potential of sea turtles in response to contemporary climate change. It is also important to consider the potential implications of adaptations and, to the extent possible, account for known non-climate-related threats which will occur concurrently and potentially synergistically so that an adaptive management approach can be undertaken in impact assessments (Fuentes et al., 2016).

Shifts in nesting phenology may result in changes in the exposure of sea turtles to threats that have a seasonal nature (e.g., specific fisheries, recreational activities). Similarly, shifts in nesting range may result in turtles being more exposed to other threats such as coastal development and sea level rise (Fuentes et al., 2020). Clearly, there are several interlinked factors affecting the ability of sea turtles to adapt and survive projected climate changes, highlighting the need for a better understanding of the cumulative and interacting nature of these factors in conjunction with animal behavior. While we address the current knowledge gaps, which hinder a more comprehensive understanding of the impacts of climate change on sea turtles (Patrício et al., 2021), there remains a need to enhance sea turtle resilience to climate change by mitigating other threats that they currently face (Brander, 2008; Fuentes et al., 2012). Such an approach will give vulnerable and depleted populations greater resilience to resist these disturbances.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest with this publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.8423088.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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CLIMATE CHANGE AND SEA TURTLE NESTING

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Can a present-day thermal niche be preserved in a warming climate by a shift in phenology? A case study with sea turtles

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How species respond to climate change may impact their extinction probability. Here we link climatology and ecology to tackle a globally important conservation question. For sea turtles, there are concerns that climate warming will cause both the feminization of populations as well as reduced hatchling survival. For 58 nesting sites across the world spanning all seven sea turtle species, we investigated whether warming might be avoided by shifts in nesting phenology to a cooler part of the year. We show that even with the most extreme phenological shift that has been reported to date—an 18-day advance in nesting per °C increase in sea surface temperature (SST)—temperatures will continue to increase at nesting sites with climate warming. We estimate that SST at nesting sites will rise by an average of 0.6°C (standard deviation = 0.9°C, $n = 58$) when we model a 1.5°C rise in SST combined with a best-case-scenario shift in nesting. Since sea turtles exhibit temperature-dependent sex determination, these temperature rises could lead to increasingly female-biased sex ratios as well as reduced hatchling production at sites across the world. These findings underscore concerns for the long-term survival of this iconic group.

1. Introduction

The pace at which animals respond and adapt to climate change may be central to their survival [1,2]. There are different means by which species may adapt to a changing environment. For example, rapid evolutionary change offers potential for adaptation for species with short-generation times, such as some plankton [3]. However, when generation times are longer (e.g. several decades), rapid genetic adaptations in the face of climate change are unlikely [4]. Range changes offer another way to adapt to a changing climate and have

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been seen widely across diverse taxa such as butterflies, plankton, birds and amphibians [5]. For species that are vulnerable to climate change but are unable to undergo rapid genetic adaptation or to change their range, other adaptive measures are needed to avoid local extinctions.

Of the seven extant sea turtle species, six appear on the IUCN Red List of Threatened Species (www.iucnredlist.org): greens (*Chelonia mydas*, globally endangered), hawksbills (*Eretmochelys imbricata*, globally critically endangered), Kemp's ridleys (*Lepidochelys kempii*, globally critically endangered), leatherbacks (*Dermochelys coriacea*, globally vulnerable), loggerheads (*Caretta caretta*, globally vulnerable) and olive ridleys (*Lepidochelys olivacea*, globally vulnerable). Flatbacks (*Natator depressus*) are classified as 'data deficient'. Climate change is impacting sea turtles in a number of ways throughout their life cycle [6]. Potential impacts range from the loss of nesting beaches due to sea-level rise and increased erosion [7] to changes in oceanic distribution due to the alteration of wind patterns and ocean currents [8]. Increased exposure to extreme thermal events (e.g. marine or air heatwaves) may also impact sea turtle foraging grounds and threaten their reproductive output [9,10]. Sea turtles have also long been considered to be at high risk from climate warming since they have temperature-dependent sex determination [11–13]. Adult females nest on beaches across the world in the tropical, sub-tropical and temperate zones [14]. They lay their eggs in nest chambers dug several tens of centimetres deep and then cover their eggs with sand. No parental care is given thereafter. Incubation typically lasts between 40 and 80 days, depending on the species and incubation temperature (e.g. [15]). Females are produced at warmer incubation temperatures [16], and so there is concern that climate warming might cause the production of highly female-skewed hatchling cohorts, which could ultimately lead to population extinction [6,17]. In addition, lower hatch success at high incubation temperatures threatens population survival [18–20]. Currently across species, most sea turtle nesting beaches around the globe produce hatchling sex ratios that are already heavily female-biased [21]. Recently, the largest green sea turtle rookery in the world was shown to be extremely female-biased [22,23].

Sea turtles have long generation times (several decades), which precludes rapid evolution of the pivotal temperature for sex determination as a means to adapt to climate change. In addition, females exhibit tight fidelity to their nesting area [24], which suggests turtles cannot readily change their range to accommodate warming temperatures [25]. Because of this tight natal fidelity and long generation time, phenological shifts in nesting (i.e. changes in the timing of nesting events) have been widely proposed as the most likely means by which sea turtles could adapt to warming temperatures [26–28]. Marked phenological changes have been observed widely across taxa (e.g. insects, amphibians and birds; [29,30]) and with sea turtles there is empirical evidence that warming temperatures can result in earlier nesting [26,27,31]. However, it is not known if the rate of phenological shifting is sufficient to mitigate future climate warming across species and populations. Here, we investigate how the thermal niche used by sea turtles is likely to change with a combination of climate warming and shifts in nesting phenology. In short, we define the current thermal niche sea turtles use at 58 rookeries across the world and project how these thermal niches would change under a scenario in which sea surface temperatures (SST) rise and turtles nest earlier in the year. We define the thermal niche turtles use with SST measurements recorded adjacent to their nesting beaches.

Previous studies have modelled how SST are likely to vary at different breeding sites within a specified timeframe (e.g. 50, 100 or 200 years) and under various climate warming scenarios (e.g. [28,32]). Here, we present a different conceptual approach and propose the question: can see turtles adapt to a 1.5°C increase in SST by shifting their nesting season to a cooler time of the year? In this manner, we consider whether phenological shifts in nesting could preserve the current thermal niche for sea turtles around the world, regardless of which climate warming scenario is followed. We projected a 1.5°C increase in SST, as this warming is very likely to happen before the end of the century (e.g. under 'Middle of the Road' scenario SSP2–4.5 it is projected that SST will increase by 1–4°C globally by 2081–2100 relative to 1850–1900; [33,34]).

2. Material and methods

2.1. Conceptual framework

We conceptualized how rising SST and a shift in nesting phenology might interact to impact future conditions (figure 1). Here we describe the conceptual framework in four steps. Details for different steps are given thereafter in §2.2.

1. We consider a seasonal cycle of SST adjacent to a sea turtle nesting area.
2. We increase the SST at each site by 1.5°C.

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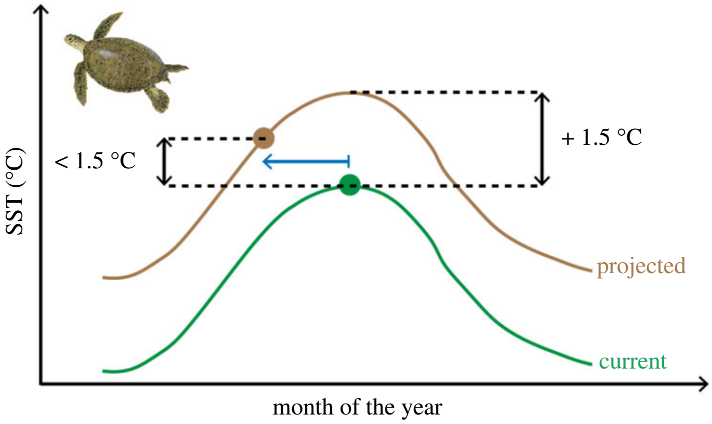

Figure 1. Conceptual framework for how a rise in SST may be mitigated by a phenological shift of the nesting season. The green and brown lines represent the current and projected SST. The filled circles represent the peak of the sea turtle nesting season. In this case, a projected 1.5°C rise in SST translates to less than 1.5°C rise in SST during peak nesting season due to a phenological shift to earlier nesting (blue arrow). The turtle image was kindly provided by NOAA Fisheries (www.fisheries.noaa.gov).

3. We shift the nesting phenology forward by 27 days (i.e. the most extreme phenological shift reported in the literature for a 1.5°C rise in SST).
4. We observe the difference between the projected and current SST during peak nesting season. If this value is less than 1.5°C we consider that part (or all) of the warming was mitigated due to the phenological shift (figure 1).

This combination of increased SST and phenological shift in nesting can potentially lead to an increase, decrease or no change in SST, depending on the nature of the seasonal change in SST and nesting seasonality. Using this conceptual framework, we parameterized the interaction of climate warming and a phenological shift in nesting for 58 sites around the world (figures 2–4).

2.2. Empirical datasets

2.2.1. Sea surface temperature

We obtained SST from the International Comprehensible Ocean-Atmosphere Data Set (ICOADS) through the National Center for Atmospheric Research (http://rda.ucar.edu/datasets/ds540.1/). The ICOADS is an extensive surface marine dataset compiled from different monitoring systems, including coastal meteorological stations, moored buoys, research vessels and surface drifters. We used the Enhanced ICOADS Monthly Summary Statistics Release 3.0.0 to obtain SST for the 2° by 2° quadrats that encompass relevant sea turtle nesting sites (i.e. the selected quadrats contained the nesting beaches as well as the area adjacent to the beaches). If a turtle rookery consisted of more than one nesting beach, we used the nesting beach with the largest turtle aggregation as the reference point around which to place the quadrat (electronic supplementary material, table S1). We used mean monthly SST recorded between January 2009 and December 2019 to describe recent annual fluctuations in SST at each nesting site. A sine function was fitted to these mean monthly SST to model year-round SST (figure 2).

To model future climate warming, we increased modelled SST by 1.5°C (figure 1) since the Intergovernmental Panel on Climate Change (IPCC) warns that a 1.5°C increase in SST is very likely to happen before the end of the century [33,34]. We compared current SST experienced during the peak of the nesting season (see point 2.2.2 Nesting seasonality, below) to projected SST after a 1.5°C increase in SST and corresponding phenological shift to earlier nesting were modelled to establish if any warming was mitigated due to the phenological shift (figure 1).

2.2.2. Nesting seasonality

We extracted nesting seasonality data and coordinates of as many sea turtle rookeries as possible from literature sources (electronic supplementary material, table S2). Sources included research articles published in peer-reviewed journals, reports from the International Union for Conservation of Nature and Natural Resources (www.iucn.org) and reports published by The State of the World's Sea Turtles

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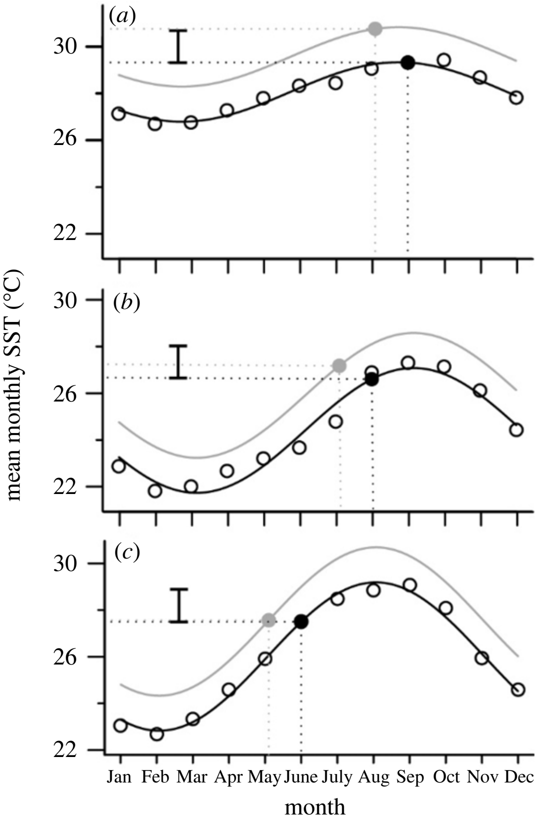

Figure 2. Phenological shifts of the nesting season have variable impacts at different sites. We modelled how a 1.5°C rise in SST combined with a 27-day advance of the nesting season would impact SST at 58 sea turtle nesting sites. Here we highlight three case examples: (*a*) On Saint Eustatius in the Caribbean, a shift of the nesting season does not mitigate any warming SST. (*b*) On Sal in the Northeast Atlantic, a shift of the nesting season mitigates approximately 60% of a 1.5°C rise in SST. (*c*) In Florida in the Northwest Atlantic (*c*), almost 100% of warming is mitigated by a best-case-scenario phenological shift. Open circles represent mean monthly SST and the black line represents the sine fit. The grey line represents projected conditions after a 1.5°C rise in SST. The filled circles represent a month during the peak of the nesting season in their respective scenarios. For easy comparison between subpanels, the vertical bars represent 1.5°C. The geographical location of these three study sites is highlighted in figure 3.

(www.seaturtlestatus.org). When different seasonality information was given for different sites, we used the most recent source. We searched for data for all seven extant sea turtle species—flatbacks, greens, hawksbills, Kemp's ridleys, leatherbacks, loggerheads and olive ridleys—including small nesting aggregations (e.g. leatherbacks nesting in Saint Eustatius, the Caribbean) as well as some of the world's largest rookeries (e.g. greens nesting in Raine Island, South Pacific). If the peak of the nesting season was not given in the publication, we assumed that the peak occurred in the middle of the nesting season, since sea turtle nesting seasons generally follow a relatively symmetric bell-shaped pattern [35].

We defined the nesting seasonality and SST for 62 nesting sites around the world, including all seven species of sea turtles (electronic supplementary material, table S2). A sine function fitted to mean monthly SST recorded between January 2009 and December 2019 described annual fluctuations in SST well at 58 out of the 62 nesting sites (i.e. the model's p-value was less than 0.05; electronic supplementary material, figure S1). We excluded from our analysis the four sites with a poor model fit (i.e. four out of 62 sites). We checked normality of the residuals through visual inspection of the residual plots. Inter-annual variability was homogeneous between months and so did not affect the model's output.

2.2.3. Phenological changes

We searched the literature for publications that report phenological shifts in nesting sea turtles (electronic supplementary material, table S3). We entered the search terms 'phenological shift' and 'sea turtle' as TOPIC in Web of Science (apps.webofknowledge.com). We did a backward and a forward citation search on relevant articles to find further articles. To provide the most optimistic scenario for how a phenological shift in nesting might help mitigate climate warming, we used the most extreme published relationship for the link between SST and nesting dates—an 18-day advance in nesting per 1°C increase

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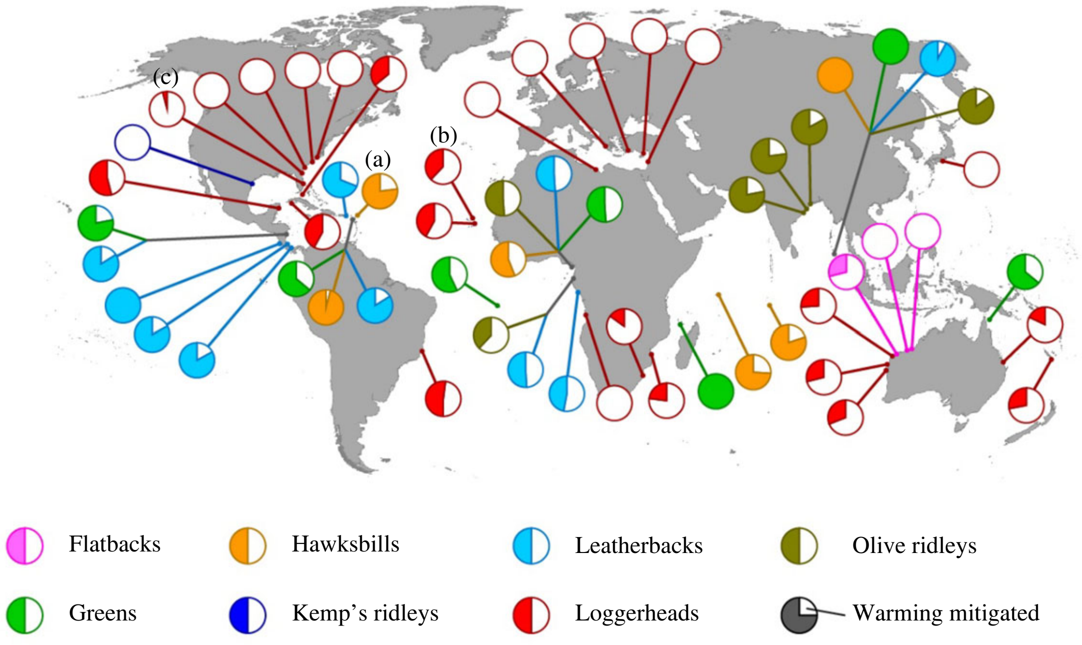

Figure 3. Global patterns for the interaction of rising SST and shifting nesting phenology. We show how a 27-day shift of the nesting in response to a 1.5°C rise in SST would affect SST at all 58 sites used in our study. The filled slice of each pie chart represents the proportion of the 1.5°C rise in SST that occurred, such that a completely full pie indicates that no warming is mitigated. Colours represent the different turtle species. The sites highlighted in figure 2 are indicated here: (*a*) Saint Eustatius (the Netherlands) in the Caribbean, (*b*) Sal (Cape Verde) in the Northeast Atlantic and (*c*) Florida (United States of America) in the Northwest Atlantic.

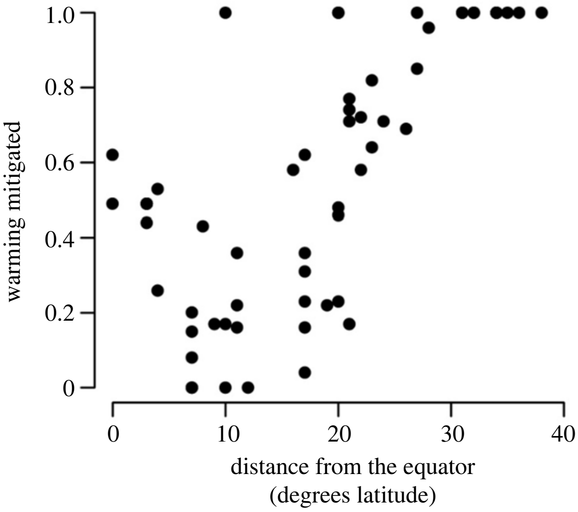

Figure 4. Phenological shifts in nesting at sites farthest from the equator have more impact on mitigating warming SST. The proportion of warming that was mitigated is plotted across sites. A 27-day shift in nesting in response to a 1.5°C rise in SST was most effective at maintaining current SST at sites greater than 30° latitude

in SST reported for loggerheads (electronic supplementary material, table S3), which translates into a 27-day advance of the nesting season for a 1.5°C rise in SST in our study.

3. Results

3.1. Sea surface temperature and nesting seasonality

In the majority of cases, sea turtles nest during the warmer months of the year (electronic supplementary material, figure S1). The northernmost nesting sites in our study were Zakynthos in Greece and Fethiye in

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Turkey, and the southernmost nesting site were KwaZulu-Natal in South Africa and Dirk Hartog Island in Australia (figure 3). 25 of the sites used in our study are loggerhead nesting sites, ten are leatherback sites, seven are green sites, six are hawksbills, six are olive ridley sites, three are flatbacks, and one is a Kemp's ridley nesting site (i.e. the only nesting site colonized without human intervention; figure 3).

3.2. Phenological changes

We found 18 relationships between SST and phenological shift from nine publications (electronic supplementary material, table S3). Relationships were given for loggerhead, leatherback and green turtles nesting at seven different sites. The longest study period was 25 years on loggerheads nesting on Zakynthos, Greece, between 1984 and 2009 [36]. The most extreme phenological change observed was an 18-day advance in nesting per 1°C increase in SST and was reported at two sites: Zakynthos, Greece [37] and Bald Head Island, United States of America [38]. We used this value to present the most optimistic scenario for how a phenological shift in nesting might help mitigate climate warming. In our study, since we are projecting a 1.5°C rise in SST, the resulting best-case-scenario phenological shift would be of 27 days.

3.3. Warming mitigated

The interaction of a 1.5°C warming and a 27-day phenological shift in nesting was variable across sites (figures 2–4). For example, a 27-day advance of the nesting season was unable to mitigate 1.5°C SST warming on Saint Eustatius (in the Caribbean; figure 2*a*). By contrast, on Sal (in the Northeast Atlantic), the same phenological shift in nesting mitigated 62% of a 1.5°C rise in SST (figure 2*b*). In Florida (Northwest Atlantic), nearly all warming was avoided by the same phenological shift (figure 2*c*). Note that we are referring here to the Peninsular Florida subpopulation (a loggerhead subpopulation defined by Loggerhead Turtle Expert Working Group), which includes nesting beaches that are geographically close and have the same nesting season ([39]; electronic supplementary material, table S1).

Rising SST were entirely mitigated by phenological shifts at 14 sites, while at four sites no warming was mitigated (figure 3). For all 58 sites, phenological shifts mitigated on average 55% of warming SST (standard deviation = 34%, min = 0, max = 100, $n = 58$; electronic supplementary material, table S4).

In addition, we found a broad latitudinal effect (logistic fit, $p < 0.05$, $r^2 = 0.49$, $n = 58$), with phenological shifts at higher latitudes having more impact on mitigating warming temperatures (figure 4). This effect likely occurs because of the more marked seasonality in SST at higher latitudes (electronic supplementary material figure S1).

4. Discussion

Climate change is having many ecological impacts, including changes in species ranges and the phenology of seasonal events such as migration and breeding [30,40,41]. While many of these changes are well described, much less clear is whether taxa can preserve their current thermal niche through the interaction of rising temperatures with changes in range or phenology [42,43]. Yet the outcome of this interaction may have strong implications for species survival, particularly when species are already threatened by various anthropogenic impacts such as habitat loss and harvesting. Our findings suggest that, all else being equal, even the maximum reported rate of phenological shift in nesting will often not be enough for sea turtles to fully mitigate rising temperatures occurring as part of climate change. Our results extend and reiterate the conclusions from previous studies at a few key sites [28,44]. Here we offer a global view of this research topic that includes all seven species of sea turtles. Additionally, a result emerging from our analysis is that the impact of a phenological shift in nesting will vary around the world, and that at higher latitudes more of the future rises in SST will likely be mitigated by phenological changes. Taken together, a key message is that we cannot assume that turtles nesting around the world will always be able to naturally mitigate climate warming impacts by a phenological shift in nesting.

Most concerning is that we explored a best-case-scenario, so it is likely that sea turtles have less adaptive potential than presented here. We likely provide an overly optimistic view of the impact of a shift in nesting, since we used the maximum reported rate for this phenological shift. Running the same analysis using the average phenological shift reported in the literature (i.e. a 9-day advance in nesting per °C increase in SST; electronic supplementary material, table S3) reveals that SST at nesting sites will rise by an average 1.0°C (standard deviation = 0.4°C, $n = 58$). Using a 4-day advance in nesting per °C increase in SST (as reported in 2009 by [45]) results in SST rising by an alarming 1.4°C (standard deviation = 0.1°C, $n = 58$).

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It may be that different species of sea turtles are not able to respond to warming temperatures in the same way. Relationships between phenological shifts in relation to sea surface temperatures were available from seven different sea turtle nesting sites (electronic supplementary material, table S3) but only for three species (i.e. loggerheads, leatherbacks and greens). Furthermore, at some sites there was no evidence for earlier initiation of the nesting in response to warmer temperatures [46]. More data are needed to better inform how different species are likely to fare in the face of climate warming. In addition, some sea turtle populations already nest at the coolest time of the year (e.g. flatback turtles nesting at Cape Domett in Australia; [47]) so a shift in the phenology of nesting will not mitigate increases in SST at these nesting locations. Indeed, a shift in phenology of nesting—if it occurred—would increase temperatures even more.

Rising SST are a threat to sea turtles because of the close relationship between SST and sand temperature, i.e. the environment in which sea turtle eggs incubate. Previous work has shown that SST and air temperature (AT) measured over large scales near nesting sites are tightly correlated with sand temperature at nest depths [48–51]. More recently it was shown that the gradients of these relationships are consistent across sites, and that for every 1°C increase in AT, sand temperature at nest depth increases by an average 0.86°C (standard deviation = 0.26°C, $n = 36$; [52]). Similarly, for every 1°C increase in SST, sand temperature increases by an average 0.72–0.83°C [48,52]. In other words, because of the tight positive relationship between SST and sand temperature it is very likely that if SST rises at one site, so will sand temperature at nest depth. In general terms, a 1.5°C rise in SST—as modelled in our analyses—would translate into approximately 1.1°C rise in sand temperatures at nest depth, although the absolute values are likely to vary slightly between sites. Due to the steep relationship between incubation temperature and hatchling sex ratio [53], a 1.1°C difference in nest temperature can be the difference between an all-male and an all-females nest, so 1.1°C is not a negligible value.

At sites around the world, it will be important to maintain empirical measurements to detect climate warming impacts on incubation conditions and so we emphasize the importance of long-term monitoring as is done in many ecosystems [54]. There are various ways in which the signs of excessive feminization might be detected. First, direct measurements of hatchling sex ratios or sand temperature at nest depths may show long-term feminization or warming respectively. Since direct measurements of sex ratios are fatal, an alternative is to estimate hatchling sex ratios using temperature-based models [55]. At sites where long-term measurements of sex ratios are not available, indications of warming might still be evident since very female-biased hatching sex ratios are accompanied by high in-nest embryo mortality [19,56] and lower hatchling quality [57–59]. Consequently, simple measures such as hatchling success (the proportion of eggs developing into hatchlings) may provide an alert to feminization that could then be substantiated by targeted measurements of hatchling sex ratios.

Because of the negative effects of warming temperatures on hatchling production and sex ratios, methods to reduce sand temperatures at nesting beaches are being explored. Strategies to artificially cool nests, such as through shading or watering, have already been trialled on different nesting beaches and offer promising results [20,60–62]. For example, shading was shown to decrease sand temperatures by an average 0.60°C on a nesting beach in Saint Eustatius (figure 2; [60]). Similarly, irrigating artificial green sea turtle nests with seawater or freshwater resulted in an immediate 1.3°C drop in nest temperatures on Heron Island (Australia; [63]). Such strategies could be implemented at sites where excessive feminization or hatchling mortality is occurring but require careful consideration. For example, there are concerns that lowering nest temperatures would alter sex ratios in a detrimental way, since having fewer females would reduce future population reproduction output [20,64]. Therefore these mitigation strategies should not only consider short-term benefits (e.g. increased hatchling production) but also promote positive long-term outcomes (e.g. population recovery or stability). Finally, it is important to note that such mitigation strategies would only offer a temporary 'Band-Aid' solution, as the underlying issues of climate change are not being addressed. Solutions to address climate change, like reducing greenhouse gas emissions, switching to renewable energies, and changing land-use patterns are required to reduce future climate change impacts.

There are clearly caveats to any predictions for how ecosystems will change in the face of climate warming, and this applies universally and not just to SST as seen in our study [65–67]. Our methods could be refined in various ways, such as by considering likely temperatures across entire nesting seasons rather than at just one point. Access to local SST datasets with better resolution and accuracy could also improve the model's output. Since variability in thermal niches exists within nesting grounds, our broad approach could also be refined for sites with inter-annual and intra-beach temperature data available. There also remain a number of uncertainties for how climate change will impact temperatures at sea turtle nesting sites. For example, there are uncertainties for how patterns of rainfall will change in

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the future [68,69]. In some nesting sites it has been shown that heavy rainfall may be sufficient to cool the sand to the extent that more male hatchlings are produced [61,70,71], so one scenario is that increased heavy rainfall may help mitigate climate warming. Second, it is possible that sea turtles might colonize new cooler nesting sites in the future. Generally, turtles have tight fidelity to their natal nesting areas, with flipper tagging showing turtles returning to broadly the same area to nest [24,72]. However, occasional breakdowns in fidelity are recorded [73–75] with, exceptionally, turtles nesting at sites 100s of km apart (e.g. [76]). Furthermore, when nesting beaches become less suitable, e.g. through increased light pollution due to development or beach erosion, turtles may shift nesting to nearby beaches [77]. It is possible that these breakdowns in fidelity could have helped with adapting to past climatic cycles, as a species' range could have expanded and contracted spatially as groups or individuals departed from philopatry. However, it remains unknown if the speed at which new sites are colonized will be sufficient to prevent feminization in nesting populations in the face of warming.

Finally, climate warming may not apply equally across seasons [78,79] and so our calculations could be refined as more information emerges on likely site-specific changes in SST seasonality. Elegant mechanistic approaches have been used to assess the drivers of incubation temperatures [47,80] and although these models are still susceptible to uncertainties on how environmental conditions such as rainfall may change [6], they provide another approach to assessing likely future changes in temperatures at sea turtle nesting sites. While both correlative and mechanistic models produce very similar results [50,81], the mechanistic approach has the advantage that it can be forced with novel combinations of environmental variables to explore different climate change scenarios. Unfortunately, it was not possible to use microclimate models in our study since the input parameters (e.g. beach properties and local meteorological data) required to run the models were not available for all study sites. However, microclimate models offer great potential in this area and may help shed further light on expected changes in incubation temperatures in the face of climate warming [47,50].

Our approach to examine how phenological shifts could mitigate climate warming can be applied broadly to other species faced with adapting to climate change. For example, our methods could be applied to other organisms that exhibit temperature-dependent sex determination, such as crocodiles and tortoises [82]. Similarly, it would be possible to assess if the rate of phenological change some migratory species exhibit would allow them to maintain their thermal niche as seasonal cycles change [83]. Since the data needed to apply our methods— i.e. temperature records, nesting seasonality data, and phenological change rates—are often commonly monitored as part of conservation and research, applying our methods could be easily done for a wide range of study organisms.

While uncertainties remain for the likely impacts of climate warming on sea turtles, our results add to the growing evidence that a phenological shift in nesting will often be insufficient, by itself, to maintain current thermal conditions [28,44]. Future work might consider how a range of processes (e.g. geographical range shifts) may buffer climate-warming impacts for sea turtles.

Data accessibility. The data are provided in electronic supplementary material [84].

Authors' contributions. J-O.L.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; G.H.: conceptualization, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. The authors declare no conflict.

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ARTICLES FOR FACULTY MEMBERS

CLIMATE CHANGE AND SEA TURTLE NESTING

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REVIEW

Climate change and marine turtles: recent advances and future directions

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ABSTRACT: Climate change is a threat to marine turtles that is expected to affect all of their life stages. To guide future research, we conducted a review of the most recent literature on this topic, highlighting knowledge gains and research gaps since a similar previous review in 2009. Most research has been focussed on the terrestrial life history phase, where expected impacts will range from habitat loss and decreased reproductive success to feminization of populations, but changes in reproductive periodicity, shifts in latitudinal ranges, and changes in foraging success are all expected in the marine life history phase. Models have been proposed to improve estimates of primary sex ratios, while technological advances promise a better understanding of how climate can influence different life stages and habitats. We suggest a number of research priorities for an improved understanding of how climate change may impact marine turtles, including: improved estimates of primary sex ratios, assessments of the implications of female-biased sex ratios and reduced male production, assessments of the variability in upper thermal limits of clutches, models of beach sediment movement under sea level rise, and assessments of impacts on foraging grounds. Lastly, we suggest that it is not yet possible to recommend manipulating aspects of turtle nesting ecology, as the evidence base with which to understand the results of such interventions is not robust enough, but that strategies for mitigation of stressors should be helpful, providing they consider the synergistic effects of climate change and other anthropogenic-induced threats to marine turtles, and focus on increasing resilience.

KEY WORDS: Climate change · Marine turtles · Sea turtles · Sex ratio · Phenology · Sea level rise · Impact mitigation · Resilience

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1. INTRODUCTION

Human-induced climate change is one of the main threats to nature and human civilization (Pecl et al. 2017, Lenton et al. 2019). Each decade since the 1980s has been warmer than any before on record, 9 of the 10 warmest years have occurred since 2005, Arctic temperatures have likely been the warmest in the last 2000 years, and atmospheric carbon dioxide is now at 414 ppm, higher than any time in more than 100 000 yr (https://climate.nasa.gov). This planetary-scale modification of the climate is having strong effects on biodiversity and ecosystems, with major impacts forecast (Newson et al. 2009, Walther 2010). Numerous

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species are already responding by changing their phenology and distribution, among other adaptations (Walther 2010, Feeley et al. 2017, Piao et al. 2019), while others are declining (Pecl et al. 2017) or have become extinct (Urban 2015, Waller et al. 2017). Notably, species responses to current rapid changes are not necessarily effective and can lead to mismatches between periodic events (e.g. breeding, wintering) and resource availability (Edwards & Richardson 2004, Post & Forchhammer 2008).

Research on the effects of climate change on biodiversity has been disproportionately centred on terrestrial organisms (Feeley et al. 2017), likely due to easier accessibility and accordingly better baseline data on both species and climate, yet numerous impacts on marine biodiversity have now been documented, from local to global scales (Poloczanska et al. 2016, Worm & Lotze 2016, Crespo et al. 2019). Most long-term studies have focussed on fish and plankton (Worm & Lotze 2016), with recent research assessing impacts on large marine megafauna (Erauskin-Extramiana et al. 2019, Albouy et al. 2020), corals (Hughes et al. 2018), seagrasses (Chefaoui et al. 2018), and seaweeds (Martins et al. 2019).

Marine turtles are a particularly interesting case study, as they have a marine and a terrestrial phase and depend on productive neritic or oceanic ecosystems for foraging, and on low-lying sandy beaches for nesting (Bolten 2003). Thus, all 7 extant species of marine turtles, which as a group are globally distributed across the Earth's tropical, subtropical and temperate marine habitats (Wallace et al. 2010), will likely be directly and indirectly affected by climate change, with impacts varying geographically, temporally, and between species and populations (Hawkes et al 2009, Poloczanska et al. 2009, Hamann et al. 2013, Fuentes & Saba 2016). Here, we present a review of the most recent literature on climate change impacts on marine turtles, providing an update since a previous similar review by Hawkes et al. (2009), to help guide future work on the topic.

2. METHODS

To identify the relevant literature, we applied the search terms 'marine turtle climate change' and 'sea turtle climate change' in Web of Science and Google Scholar, and then used the 'snowball' approach, by thoroughly searching both the literature cited in these articles and the articles in which they were cited. We then screened the abstracts of each article and rejected papers that were not related to climate change and marine turtles. The papers that were kept were categorized by habitat, climate change threat, expected climate change impact, species, and geographic location. Papers previously reviewed by Hawkes et al. (2009), which were published between 1988 and April 2009 (n = 54), were also categorized in the same manner and referred to as the 'original database'. Throughout this review, we summarize where most research on this topic has focussed (Section 3), review the most recent studies assessing climate change impacts on different marine turtle life stages/parameters (Section 4), outline management strategies to reduce predicted impacts (Section 5), and set research priorities to improve our knowledge on how climate change may impact marine turtles (Section 6).

3. SUMMARY OF MAIN RESEARCH TOPICS

Interest in the impacts of climate change on marine turtles has increased (Fig. 1), and we found 202 peer reviewed papers on this subject, published from May 2009 to October 2020, representing 76% of all the peer-reviewed papers on this topic since 1988. Overall, the main areas of research were consistent between the new and the original database, for all categories, and are summarized in Fig. 2. Considering both the 'original database' (1988–2009) and the new database (2009–2020), by far, most research was focussed on the terrestrial phase only (Fig. 2). Considering climate-change-induced threats to marine turtles or their habitats, during both periods, the

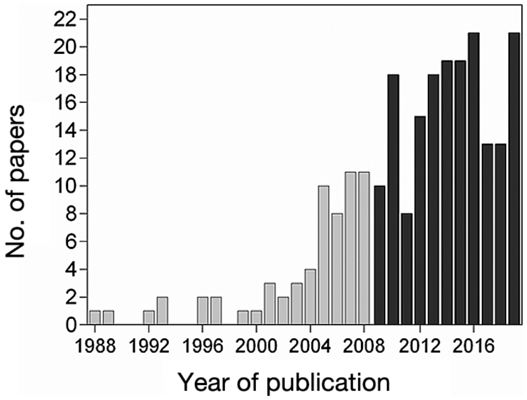

Fig. 1. Number of peer-reviewed studies per year on climate change impacts on marine turtles; grey bars: studies published between 1988 and April 2009 and reviewed by Hawkes et al. (2009), black bars: studies published from May 2009 to December 2019. Publications from 2020 are not included in the figure (although they have been reviewed in the article), as the numbers would not be representative of the whole year

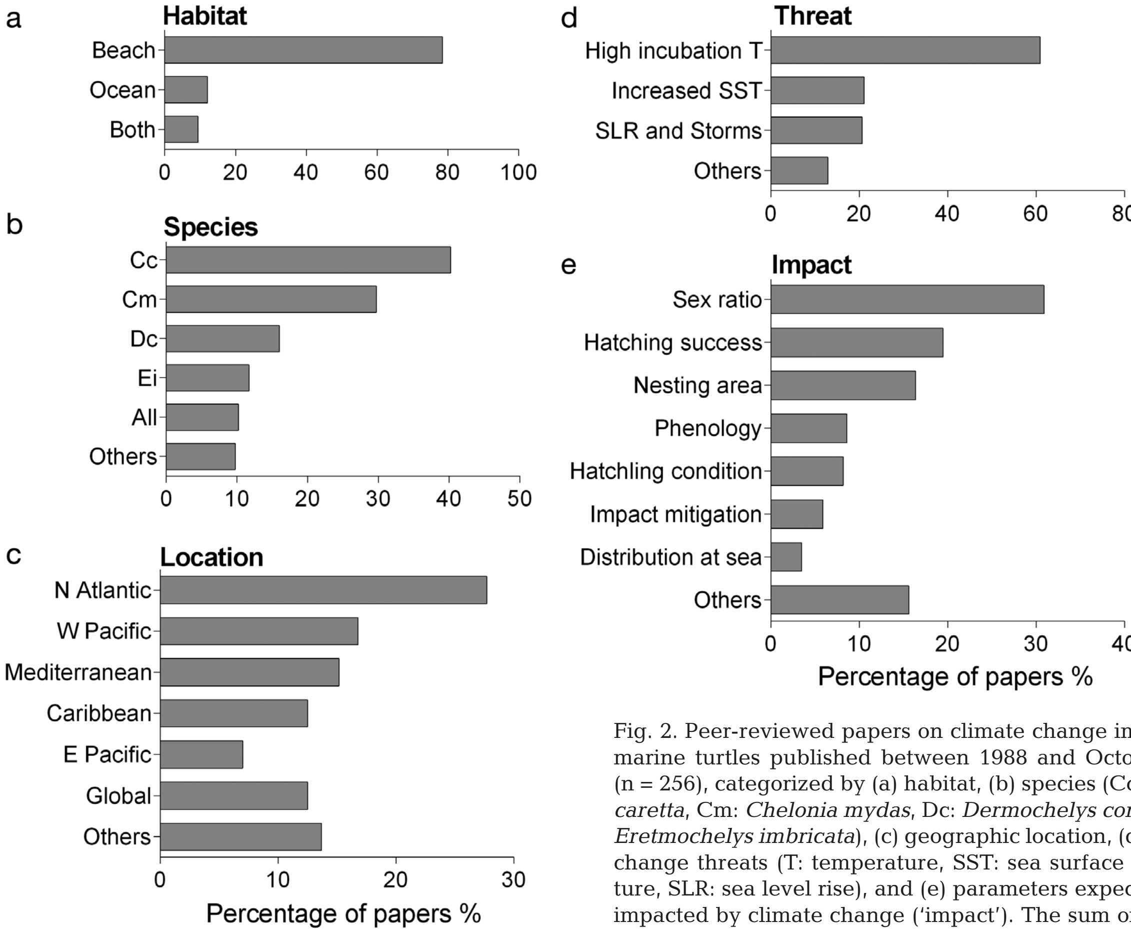

Fig. 2. Peer-reviewed papers on climate change impacts on marine turtles published between 1988 and October 2020 (n = 256), categorized by (a) habitat, (b) species (Cc: *Caretta caretta*, Cm: *Chelonia mydas*, Dc: *Dermochelys coriacea*, Ei: *Eretmochelys imbricata*), (c) geographic location, (d) climate change threats (T: temperature, SST: sea surface temperature, SLR: sea level rise), and (e) parameters expected to be impacted by climate change ('impact'). The sum of the percentages can be above 100%, as some papers assess more than 1 species, location, threat, or impact

future increase in incubation temperatures received the most attention, followed by sea level rise and storms and by increases in sea surface temperature (SST). As for the potential impacts from climate change, biased sex ratios were the most addressed during the both periods, followed, in the new database, by reduced hatching success, loss of nesting area, hatchling morphology, survival and performance ('hatchling condition' in Fig. 2), changes in breeding phenology, and strategies for impact mitigation. In the original database, the most researched impacts after biased sex ratios were changes in movements and distribution at sea, reduced hatching success, and changes in breeding phenology. Loggerhead turtles *Caretta caretta* and green turtles *Chelonia mydas* were the most researched species during both periods. Lastly, when considering the geographic distribution of studies, most focussed on the North Atlantic, the West Pacific, the Mediterranean, and the Caribbean, with a small number of global assessments.

4. CURRENT KNOWLEDGE, RESEARCH ADVANCES, AND KNOWLEDGE GAPS

Throughout this section, we recap the base knowledge on how climate change can impact different life-stages/parameters (Fig. 3), we review the most recent literature, highlight research advances made in the last 11 yr, assess knowledge gaps, and briefly suggest ways forward to improve our knowledge on the impacts of climate change on marine turtles.

4.1. Sex ratios

The effects of climate change on the primary sex ratio of marine turtles, i.e. the sex ratio of offspring, was the first parameter that researchers warned would be affected by climate change (Davenport 1989, 1997, Janzen 1994, Mrosovsky 1994). Since marine turtles have temperature-dependent sex determination (TSD; Yntema & Mrosovsky 1980,

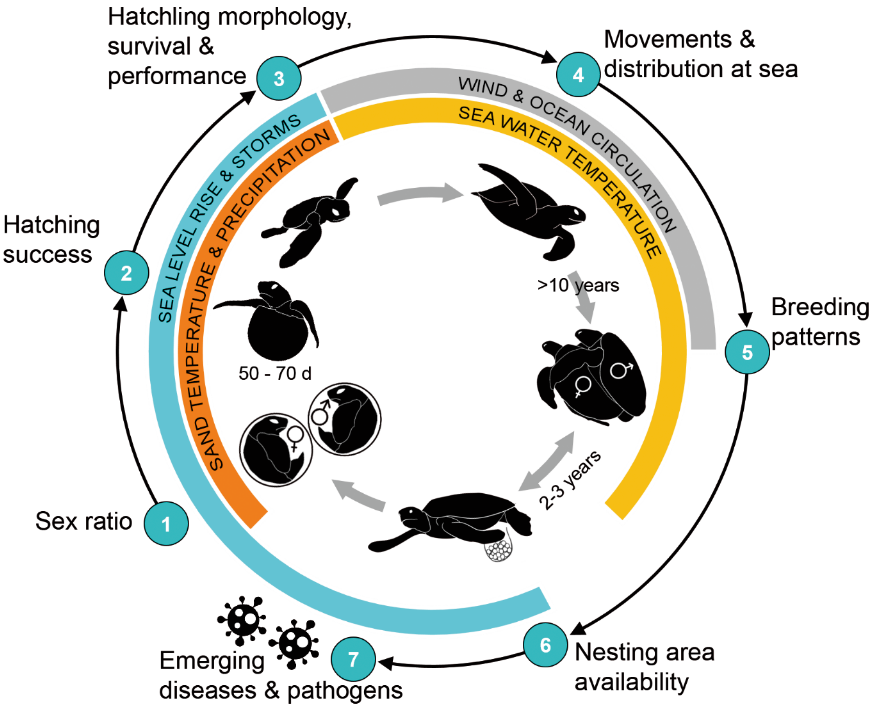

Fig. 3. Generic life cycle of marine turtles with parameters expected to be impacted by climate change as reviewed in Section 4. Predominant associated climate threats are noted. Parameter numbers link to subsection numbers in Section 4

Ackerman 1997), it is predicted that increases in incubation temperatures will eventually lead to feminization of some marine turtle populations (Janzen 1994, Santidrián Tomillo et al. 2015a). The majority of studies estimating current primary sex ratios reported female biases, for all species of marine turtles in all ocean basins in which they occur (e.g. Mrosovsky & Provancha 1992, Godfrey et al. 1996, Binckley et al. 1998, Hanson et al. 1998, Broderick et al. 2000, Sieg et al. 2011, King et al. 2013, Binhammer et al. 2019, Monsinjon et al. 2019a, Tanner et al. 2019), with few reports of balanced to slightly male-biased primary sex ratios (Stubbs et al. 2014, Esteban et al. 2016, Patrício et al. 2017, Laloë et al. 2020). Thus, when modelling primary sex ratios of marine turtles under future climate change scenarios, several studies projected that male production may cease in the near future (2100; e.g. Janzen 1994, Hawkes et al. 2007a, Witt et al. 2010, Monsinjon et al. 2019a), particularly in populations that are already producing extremely female-skewed primary sex ratios (Hays et al. 2017, Monsinjon et al. 2019a, Tanner et al. 2019). For example, in one of the world's largest green turtle populations (northern Great Barrier Reef, Australia; Limpus 2008), 99.1% of the juveniles, 99.8% of the subadults, and 86.8% of the adults were estimated to be female (Jensen et al. 2018), suggesting that the primary sex ratio has been increasingly female skewed for around 20 to 30 yr (Chaloupka et al. 2004), with projections indicating the future feminization of this population (Fuentes et al. 2010a).

4.1.1. Direct methods to identify the sex of hatchlings: from the examination of gonads to molecular clues

Determining primary sex ratios currently requires sacrificing hatchlings for histological examination of gonads. This is ethically challenging given that most marine turtle species are protected in many countries. Laparoscopy is a non-lethal alternative (Wyneken et al. 2007), but is a highly skilled procedure, and is labour and resource intensive, as sexing cannot be carried out until hatchlings are several months old (Wyneken & Lolavar 2015). Consequently, several studies have explored the potential of molecular markers, such as the accumulation of sex steroid hormones in the plasma of neonates (Gross et al. 1995), in the amniotic fluid from the egg (Xia et al. 2011), and in eggshells (Kobayashi et al. 2015), to identify the sex of marine turtle hatchlings, with reports of high levels of agreement in sex identification between hormone ratios and gonad histology observations. Other studies have looked at temperature-dependent expression of an RNA-binding protein in gonads (Tezak et al. 2017), and at compounds expressed at either male- or female-promoting temperatures (e.g. Anti-Müllerian hormone and CYP19A1 aromatase, respectively, Tezak et al. 2020a). These methods are promising and could facilitate the identification of sex ratios in the field, but will be limited to researchers who have access to the analytical skills and facilities required to run such samples at large scales, and their application at ecologically relevant spatial (beaches) and temporal (nesting seasons) scales may remain unrealistic in the near future. Further, testing and modelling tools and the potential for low-cost field assays are required to properly extrapolate this critical population parameter under climate change scenarios.

4.1.2. Indirect methods to predict primary sex ratios: scaling up from a clutch to the entire beach

Given the challenges in directly assessing the sex of hatchlings, the majority of studies to date have relied on estimating primary sex ratios from either local air, sea surface, and/or sand temperature, or temperature measured inside egg clutches, often also estimating metabolic heating and the extent of thermal heterogeneity within the nest (Girondot & Kaska 2015, Monsinjon et al. 2017a,b, 2019a, Laloë et al. 2020). At the scale of an embryo, sex is determined by temperature during a thermosensitive period of development (TSP, Mrosovsky & Pieau 1991), which falls during the middle third of incubation under constant incubation temperatures. This has often led to the use of the mean nest temperature during the middle third of incubation to predict sex ratios (e.g. Sieg et al. 2011, Fuller et al. 2013, Laloë et al. 2014, 2016, Sarı & Kaska 2015, Esteban et al. 2016, Yalçin Özdilek et al. 2016). More recent work shows that (1) the TSP shifts away from the middle third of incubation in field conditions (i.e. under variable thermal conditions, Girondot & Kaska 2014) and that (2) the mean temperature does not account for the role of embryonic growth during sex determination (Fuentes et al. 2017, Girondot et al. 2018), so previous models have now been improved by incorporating these adjustments. Additionally, sex ratio estimates have been found to vary depending on the metric used (i.e. temperature-based or duration-based) and the period over which it is calculated (whole incubation, middle third of incubation or actual TSP, Fuentes et al. 2017). It has been suggested that the constant temperature equivalent (CTE, Georges 1989, Georges et al. 1994), defined as the temperature above (or below) which 50% of development occurs, is a better metric (Fuentes et al. 2017). This method has benefited from considerable improvements in recent years, specifically: an understanding of reaction norms that describe the progression of embryonic growth during incubation (Georges et al. 2005, Mitchell et al. 2008, Woolgar et al. 2013, Stubbs et al. 2014), a non-linear embryonic growth function (Girondot & Kaska 2014), a TSP based on embryonic stages (Fuentes et al. 2017, Girondot et al. 2018), and a new formulation of the CTE ($\text{CTE}_{\text{GROWTH}}$) that accounts for changes in the rate of embryonic growth (Fuentes et al. 2017). The $\text{CTE}_{\text{GROWTH}}$ model (e.g. using the R package 'embryogrowth', Girondot 2020a) can be used to predict the sex ratio of a clutch based on the TSD reaction norm (also called sex ratio thermal reaction norm) if it has been derived from constant-temperature incubation experiments for the same population (see Abreu-Grobois et al. 2020 for a review of existing models).

Notably, to extend primary sex ratio estimates at the scale of an entire rookery, additional scaling parameters must be taken in consideration, because nests can experience different incubation conditions on the same beach depending on thermal microhabitats (Fuentes et al. 2010a, Patrício et al. 2017, Flores-Aguirre et al. 2020). Microclimate models (e.g. NicheMapR; Kearney & Porter 2017) are promising and can be used to explicitly characterize the heterogeneity of sand temperatures due to beach topography, shade, moisture, presence of vegetation, and beach-specific substrate physical properties (Fuentes & Porter 2013, Stubbs et al. 2014, Bentley et al. 2020, Laloë et al. 2020). However, these models require that some parameters are measured *in situ* for adequate calibration (e.g. moisture content, gravimetry), yet default parameters are sometimes used when no empirical measurements are available (but see Bentley et al. 2020). Additionally, implementing metabolic heating in microclimate models may be an important step forward since the heat produced by growing embryos increases the temperature of nests relative to their surrounding environment (Booth & Astill 2001, Broderick et al. 2001a), and models have to be properly parametrized for coastal environments (Bentley et al. 2020). Lastly, studies normally produce estimates of primary sex ratios from a subset of clutches, which are then used to indicate the primary sex ratio for a whole rookery and in some cases are used to infer population-level trends (e.g. Mrosovsky & Provancha 1989, Kaska et al. 2006, LeBlanc et al.

2012). In the future, including clutches laid at the beginning and end of nesting seasons, and multi-season data from a variety of beaches, will allow insights that fully capture seasonal variation. Some promising studies recently benefitted from sophisticated nesting dynamic models (Girondot 2017) to hindcast or forecast primary sex ratios of loggerhead and green turtle nesting populations (Monsinjon et al. 2019a, Laloë et al. 2020). This remains to be conducted for other marine turtle rookeries worldwide.

4.1.3. Understanding TSD under natural conditions

Despite the volume of research focussed on the effects of climate change on the sex ratio of hatchlings, several knowledge gaps still exist. First, in a key review, Wyneken & Lolavar (2015) showed that the majority of studies published to date have derived sex ratio estimates from 'second and third level proxies', for example estimating sex ratio from mean nest temperature or from incubation duration, respectively. Comparatively few studies have carried out hatchling gonad histology to verify sex directly (a 'first-order proxy') and even those that have, likely statistically under-sampled each clutch and lack evidence to suggest that the sampled individuals properly represent the sex ratio of the whole clutch in question, let alone the rookery (Wyneken & Lolavar 2015). Because of the lack of such studies, it is not clear how much variation there may be in pivotal temperatures, the transitional range of temperatures, and the slope of the relationship between temperature and sex ratio (i.e. parameters of TSD reaction norms) between individuals, rookeries, and ocean basins. How widely can an equation relating nest temperature to resultant sex ratio be applied? This question clearly reveals a gap in our understanding of TSD under natural conditions, as our assumptions mostly rely on constant-temperature incubation experiments in laboratory conditions (even sometimes relying on data from a different population). Several studies have attempted to estimate TSD reaction norms from field data, such as mean nest temperatures (e.g. Kaska et al. 1998, 2006, Öz et al. 2004, LeBlanc et al. 2012, Patrício et al. 2017) or incubation durations (e.g. Godley et al. 2001, Fuller et al. 2013, dei Marcovaldi et al. 2014, Sarı & Kaska 2015). However, these approaches are likely biased since they do not account for uncontrolled sources of variation (e.g. genetic background and maternal effect) and compounding effects of fluctuating temperatures when multiple nonlinear and nonmonotonic reaction norms are involved (known as Jensen's inequality; Ruel & Ayres 1999, Martin & Huey 2008, Denny 2017), as it is the case for sex determination in the freshwater turtle *Chrysemys picta* (Neuwald & Valenzuela 2011). We urge future studies to bridge this gap and allow for the estimation of TSD reaction norms from *in situ* temperature data. This research area should benefit from the recent development of promising sexing techniques (Tezak et al. 2017, 2020a) that will considerably facilitate the estimation of sex ratios from *in situ* nests at broad spatial and temporal scales.

Importantly, some studies have presented evidence that nest humidity may play an underappreciated role in modifying sex ratios, and that a male bias can be produced at 'female-producing' incubation temperatures if clutch humidity is high (Wyneken & Lolavar 2015). This is likely due to evaporative cooling (Lolavar & Wyneken 2017, 2020); further studies will allow us to clarify the mechanism behind these observations, as this is a major avenue for future research (Sifuentes-Romero et al. 2018).

4.1.4. Reconstructing past and future nest temperature

How we trust primary sex ratio predictions under scenarios of changing climates depends on the reliability of reconstructed nest temperatures. Two approaches are commonly used to predict nest temperatures: either a correlative approach (i.e. linear relationships between sand or nest temperature and environmental variables) or a mechanistic (process-explicit) approach (i.e. heat balance equation, accounting for heat transfers via radiation, convection, conduction, and evaporation). Both approaches have limitations that require further investigation. Many studies also either predict sand temperatures at nest depth (i.e. without accounting for metabolic heating) or incubation temperatures experienced by embryos within nests. Correlative models likely provide reasonably accurate estimations of average daily temperature in the middle of the clutch (Fuentes & Porter 2013, Girondot & Kaska 2015, Monsinjon et al. 2019a, Laloë et al. 2020) but may not be useful outside of the ranges over which the original models were fitted (Fuentes & Porter 2013, Bentley et al. 2020), which reduces their applicability under scenarios of changing climates. Air temperature has been widely used for nest temperature predictions (Hays et al. 2003, Laloë et al. 2014, 2016, 2017, Esteban et al. 2016, Patrício et al. 2017, 2019), and SST may improve estimates (Fuentes et al. 2009, Girondot & Kaska 2015, Bentley et al. 2020), while other variables (e.g. sand moisture, cloud cover, precipitation, influence of vegetation, wind speed) are yet to be accounted for. On the other hand, mechanistic models (Fuentes & Porter 2013, Stubbs et al. 2014, Cavallo et al. 2015, Whiting et al. 2018, Bentley et al. 2020, Laloë et al. 2020) hold potential for sand temperature predictions at specified depths, provided that required input data (e.g. sand physical properties, beach topography, meteorological variables) are available. However, this makes such models difficult to run at large spatial and temporal scales, since physical properties could differ greatly across nesting beaches, and local weather conditions are often at remote sites and can only be predicted with limited confidence for the future. In addition, the only model used so far for marine turtles (NicheMapR microclimate model, Kearney & Porter 2017) was initially developed for terrestrial ectotherms and thus cannot yet account for other coastal physical processes (Bentley et al. 2020), such as tidal movements and wave action.

The choice of input data used to drive a model (being correlative or mechanistic) is also a critical step. So far, the field has not considered environmental variation at spatial and temporal scales that are relevant for marine turtles. For instance, monthly mean temperatures derived from global climate datasets have previously been used to project sand temperatures (Laloë et al. 2014, 2016, 2017, Esteban et al. 2016). Yet short-term exposure to high temperatures can lead to a higher proportion of females than what would be expected from average temperatures (Georges 1989, Georges et al. 1994), and rainfall spikes throughout a nesting season can provide short periods of cooling and thus decrease incubation temperatures (Houghton et al. 2007). Daily beach-scale temperature variations have important implications for biological and ecological processes (Ruel & Ayres 1999, Martin & Huey 2008, Denny 2017, 2019), including incubation and sex determination in marine turtles. Using daily temperatures should improve both correlative and mechanistic models (Monsinjon et al. 2019a, Laloë et al. 2020). Additionally, global climate reanalysis products can be used to provide a clear picture of thermal microhabitats (Carter et al. 2015), according to species' size and ecology, thus avoiding spatial mismatches between the size of organisms and the scale at which climate data are modelled (Potter et al. 2013). We encourage future studies to (1) thoroughly characterize nesting beach microclimates that comprise the spatial and temporal distribution of clutches for a population using *in situ* temperatures and local weather data, and (2) take advantage of the latest release of gridded climate datasets with the finest spatial (<0.5° × 0.5°) and temporal (<daily) resolutions (e.g. ECMWF ERA5 reanalysis; Hersbach et al. 2019), for a better understanding of the physical and meteorological processes at play in such highly dynamic environments (land–sea interface). Achieving such model improvements should enhance our ability to predict primary sex ratios with better accuracy, and at finer spatio-temporal scales.

4.1.5. Population persistence under female-biased sex ratios

How seasonal primary sex ratios translate into adult sex ratios remains largely unknown and may vary within and among species (Hawkes et al. 2009, Hamann et al. 2010, 2013). Recent studies suggest that some populations with female-biased primary sex ratios have balanced or male-biased adult sex ratios (Schofield et al. 2017, Lasala et al. 2018). Importantly, whether there are sex-specific differential mortalities across age classes requires further investigation. For instance, male leatherback turtle *Dermochelys coriacea* hatchlings may exhibit higher fitness than females (Rivas et al. 2019), while adult loggerhead females might exhibit higher annual survival rates than males (Schofield et al. 2020).

If adult sex ratios were to become extremely skewed, population-wide detrimental effects, such as reduced fertilisation rates (Bell et al. 2010) and increased genetic drift via a reduction of effective population size (Girondot et al. 2004), could theoretically occur. However, the operational sex ratio (OSR), i.e. the proportion of males and females successfully breeding each year, is likely to differ from the adult sex ratio in marine turtles because males may breed annually with several females, while females do not breed every year (Hays et al. 2010a, 2014, Casale et al. 2013). The OSR is currently best estimated by genetically reconstructing parentage of nests to identify the number of male sires (Wright et al. 2012a, Phillips et al. 2013). This approach provides a robust estimation of the OSR because marine turtles, unlike freshwater and terrestrial turtles, do not generally store sperm between nesting seasons that they could use to fertilise clutches in years without males present (Phillips et al. 2013, 2014, 2017, Sakaoka et al. 2013). For instance, a ratio of 1.3 breeding males for each nesting female was determined at a fine scale using genetic reconstruction of paternity in 94 green turtle nests (from an estimated 92% of all turtles nesting at the study rookery) across 3 years (Wright et al. 2012a,b). Other studies have reported similar relatively balanced to male-biased OSRs (Hays et al. 2010a, Lasala et al. 2013, 2018, Schofield et al. 2017). Additionally, multiple paternity has been demonstrated in all 7 species of marine turtles (Lee et al. 2018), varying from 9% in hawksbill turtles *Eretmochelys imbricata* (Phillips et al. 2013) to 93% in loggerhead turtles (Zbinden et al. 2007), likely as a consequence of the incidence of male–female encounters (Lee et al. 2018). It thus seems sensible to suggest that male turtles are not currently scarce at breeding grounds.

Female bias in primary sex ratios in marine turtles is frequently referred to as a vulnerable life history trait, whereas there is no evidence at present to suggest this is true. A female-biased sex ratio could benefit populations in the short-term by enhancing their growth rate (Rankin & Kokko 2007, Boyle et al. 2014a, Hays et al. 2017, Patrício et al. 2019); however, sustained warming could overrun this demographic advantage (Saba et al. 2012, Laloë et al. 2014, Santidrián Tomillo et al. 2015a). Either way, an important question is yet to be elucidated: under what range of adult sex ratios is the persistence of populations maximized? Modelling studies indicate that we can expect enhanced population growth and range expansion in reptiles with TSD under a warming scenario, assuming male dispersal and no shortage of breeding males (Boyle et al. 2014a,b, 2016). Male-biased dispersal is likely to be the rule in marine turtles, as suggested from male-mediated gene flow (Karl et al. 1992, Casale et al. 2002, Bowen & Karl 2007), and could prevent highly female-biased populations from collapsing (Doody & Moore 2010, Boyle et al. 2016). Thus, TSD in marine turtles could allow for a coadaptation mechanism, by enhancing the fecundity of a population (through female production) when hatching success is lowered under extreme high temperatures (Santidrián Tomillo & Spotila 2020). However, whether those highly female-biased populations have (or will) become population sinks (i.e. population numbers falling below replacement level) needs to be investigated. In addition, Boyle et al. (2016) suggested that 3°C warming over the next 100 yr may be a ceiling at which population declines should be expected to occur for species with TSD, but also that in reptiles with a male/female TSD reaction norm, it may be possible to model what the optimal marine turtle adult sex ratio should be. Thus, although the impacts of climate change on marine turtle primary sex ratio have been widely studied, we suggest that much work remains to be done to fully understand how this parameter might be affected and elucidate the resultant consequences.

4.2. Hatching success

Hatching success (the proportion of eggs that produce viable hatchlings) can be highly variable within and between species, but rates in excess of 65% of eggs producing viable hatchlings appear to be normal (Bell et al. 2010). However, if even small changes to the nest environment occur at the upper end of the incubation range of temperatures, they can affect hatching success. For example, at incubation temperatures above 30°C, an increase to 31°C can decrease hatching success by up to 25% (reviewed by Howard et al. 2014). The lethal upper thermal limit that embryos can withstand and still successfully hatch appears to vary within and between species (Pike 2014). Additionally, this threshold seems to depend on the duration over which the eggs are subjected to high temperatures, and it can be modulated by rainfall and nest humidity (Lolavar & Wyneken 2017). If mean incubation temperatures are above 35°C, hatching success may be close to zero, but nests can experience higher transient temperatures (e.g. 37°C) without them being lethal (Howard et al. 2014). In the context of climate change, the lethal upper thermal limit is extremely important to determine, because it underlies modelling efforts to predict the proportion of nests that may become unviable in the future (Hawkes et al. 2007a, Laloë et al. 2017, Laloë & Hays 2017, Monsinjon et al. 2019a, Tanner et al. 2019).

A thorough characterization of thermal microhabitats should elucidate temperature-induced incubation failure, which is important because some warmer 'female-producing' clutches might approach lethal temperatures more often (and thus experience higher mortality rates) than cooler 'male-producing' clutches. For example, models of thermal tolerance that allow for the estimation of both lower and upper lethal temperature thresholds could be useful when extrapolating primary sex ratios under shifting phenology scenarios towards cooler or warmer parts of the year (Monsinjon et al. 2019a). To date, most of the published estimates of upper thermal threshold limits are from loggerhead and green turtles (e.g. Matsuzawa et al. 2002, Weber et al. 2012, Read et al. 2013), but perhaps more importantly, the mechanistic basis for decreasing hatching success with increasing mean incubation temperature is not understood for any species. It may relate to oxygen availability within the nest (Ackerman 1980) but may also relate to increases in abnormalities that inhibit development (Packard et al. 1977). Surprisingly, with few exceptions (Chen et al. 2010, Cheng et al. 2015, Stewart et al. 2019), there is a lack of studies using oxygen sensors in turtle nests, and the rates of abnormality in failed hatchling turtles have yet to be synthesised across species and populations. An important research line is the possibility of increasing thermal tolerance as a response to climate change. Tedeschi et al. (2016) assessed the capacity of loggerhead embryos to adapt to increasing temperatures, by assessing the expression of heat shock-genes, which mitigate damage to cells under heat stress. They found within-clutch plasticity in gene expression and showed that this plasticity was heritable, thus demonstrating the presence of molecular mechanisms for tolerating and, potentially, adapting to future rises in incubation temperatures (Tedeschi et al. 2016).

Average humidity and accumulated precipitation also affect hatching success (Santidrián Tomillo et al. 2012, Rafferty et al. 2017, Montero et al. 2018a). At drier sites, heavy rainfall was shown to increase hatching success, while the opposite was observed at high-humidity sites (Santidrián Tomillo et al. 2015b, Montero et al. 2019). Future increases in extreme weather events with protracted rainfall may enhance hatchling production at temperate beaches and lower it at tropical beaches (Montero et al. 2019). Additionally, Rivas et al. (2018) noted that deeper nests suffered higher mortality due to increases in the water table, so interactions between biological (e.g. nest depth, location) and environmental factors should be considered.

In summary, because the eggs of marine turtles incubate at the mercy of their local environment (Miller 1997), overall patterns of hatching success are related to local climatic factors such as temperature, rainfall, inundation, and storminess (Caut et al. 2010, Santidrián Tomillo et al. 2012, Ahles & Milton 2016, Montero et al. 2018a,b, 2019), but the effect of climate appears to be variable (Santidrián Tomillo et al. 2015b) and may not entirely explain hatchling production failure (Rafferty et al. 2017). Metabolic heat can also significantly increase incubation temperatures towards the end of development, and therefore impact hatching success (Zbinden et al. 2006, Gammon et al. 2020). Future work could seek to comprehensively describe how local climate influences the incubation environment in detail, i.e. not using a single average nest temperature but describing the full variation in temperature between all eggs in a clutch, along with humidity and groundwater inundation, and consider metabolic heating as well (Gammon et al. 2020).

4.3. Hatchling morphology, survival, and performance

In both freshwater and marine turtles, incubation temperature has been shown to affect hatchling size and locomotory performance (on land and in water, Booth 2018), as well as the prevalence of scute abnormalities (Miller 1985, Reid et al. 2009, Telemeco et al. 2013). This is to be expected because the rates at which biochemical reactions take place increase at warmer temperatures (Vleck & Hoyt 1991). Maximal rates of oxygen consumption during development are higher in warmer loggerhead turtle nests (Reid et al. 2009), and embryonic development is thus likely also faster. However, because cooler nests incubate over a longer duration, it appears that more yolk is converted to somatic tissue (hatchlings have less residual yolk left at hatching), and consequently hatchlings from cooler nests appear to be marginally larger, but usually about the same mass (reviewed by Booth 2018). Additional work on this topic (Booth & Evans 2011, Maulany et al. 2012, Fisher et al. 2014, Horne et al. 2014, Sim et al. 2015, Rivas et al. 2019, Salleh et al. 2019) has suggested, however, that the effect of incubation temperature on hatchling size and locomotory performance is likely small. The impact of incubation temperature on hatchling morphology, survival, and performance has now been investigated in 5 of the 7 marine turtle species (to date there appear to be no studies on hawksbill or Kemp's ridley *Lepidochelys kempii* turtles), and the basis and consequences of these differences (e.g. whether a larger body size confers better defence against gape-limited predators) remains to be demonstrated for any population of marine turtles. The effect of moisture has been less studied, but a positive correlation between moisture and hatchling size was recently observed in natural nests (Tezak et al. 2020b).

Hatchling marine turtles are precocial and need to be capable of escaping predators from the moment they leave their nest, and thus rapid terrestrial and aquatic dispersal to offshore habitats is a key life history trait (Booth 2018). The relationship between incubation temperature and performance appears to be complex, likely an inverted 'U'-shaped relationship, where performance optima lie at intermediate temperatures (likely between 28 and 32°C; Booth 2017, 2018). This means that as ambient temperatures increase above this optimum with climate change, hatchlings (which are more likely to be female at warmer temperatures) could perform more poorly in the initial hatchling frenzy. Studies examining terrestrial dispersal tend to use 2 metrics to quantify performance: righting from dorsal recumbency (which simulates tripping over beach obstacles) and running speed. To date, the effect size measured appears to be relatively small and variable (e.g. varying between 0.08 and 11.5 s longer to right, Maulany et al. 2012, Staines et al. 2019; and between 0.5 m s^{-1} slower and 1.5 m s^{-1} faster, Sim et al. 2015, Rivas et al. 2019) and is almost certainly complicated by species differences and rookery to rookery variation in physiological parameters. Other reptiles (e.g. freshwater turtles, lizards, and snakes) have varying directions of change in locomotor performance as a result of warmer incubation conditions (reviewed by Booth 2006), and future comparative studies between marine turtles and other reptile groups may prove fruitful for identifying underlying drivers. For a variable that is so easy to measure, it is surprising that there are still few studies for marine turtles, on limited numbers of nests, to facilitate such a comparison.

Swimming performance in hatchling turtles has been less studied to date, with most studies focussing on green turtles (Booth et al. 2004, Burgess et al. 2006, Ischer et al. 2009, Booth & Evans 2011). Hatchlings swimming in water do not appear to exhibit symptoms of thermal stress until 41.7°C, which is outside of the range normally measured in natural nests and certainly far warmer than experienced in seawater (Drake & Spotila 2002). Hatchlings from warmer nests have between 5 and 12% higher stroke frequency (the rate at which hatchlings flap their flippers) than hatchlings from cooler nests when swimming in the same temperature water (Booth et al. 2004, Burgess et al. 2006, Ischer et al. 2009), but water temperature has a 3–4 times greater effect on stroke frequency, so the nest temperature effect is dwarfed in comparison (Booth & Evans 2011). This is because water temperature has a strong effect on whole-body metabolism in ectotherms (Ultsch 2013); for example, loggerhead turtle metabolic rates increase 2.4- to 5.4-fold for a 10°C increase in water temperature (Lutz et al. 1989, Hochscheid et al. 2004). Hatchlings from warmer nests appear to produce lower mean thrust per flipper beat than hatchlings from cool nests (Booth & Evans 2011), suggesting that some physiological property unrelated to metabolism may differ with incubation temperature – for example, that the swimming muscles of hatchlings from warmer nests may have fewer 'fast twitch' Type II muscle fibres, which produce greater peak force (Hill et al. 2012), or that hatchlings from warmer nests may have proportionally fewer mitochondria, or lower capillary to muscle fibre ratios (thus supplying less oxygen to each muscle fibre). In addition, some limited evidence (Fisher et al. 2014) suggests that the proportion of time spent power stroking (the dominant propulsive swimming stroke) may be reduced with nest incubation temperature, which could suggest that hatchlings from warm nests could have less 'slow-oxidative' Type I muscle fibres, which produce lower peak forces, but fatigue more slowly. An understanding of how these physiological properties change with the incubation regime, and how they may be genetically encoded, will be fundamental to unravelling the downstream fitness consequences of the incubation environment. It is of note that such measurements would be necessarily invasive (requiring hatchling sacrifice) but would likely yield significant additional insights to complement the non-invasive work that has been completed.

4.4. Movements and distribution at sea

The behaviour and spatial distribution of marine turtles are largely affected by seawater temperature and ocean circulation patterns (Luschi et al. 2003, Hawkes et al. 2007b). As marine turtles migrate over thousands of kilometres (Plotkin 2003, Godley et al. 2008), and carry out variable foraging strategies throughout their life cycle (Bolten 2003), climate change impacts and potential responses may vary across ontogenetic stages and habitats.

Being ectothermic, seawater temperature can radically impact marine turtle physiology (Milton & Lutz 2003). Normal vital function is probably impaired below a thermal threshold of around 10–15°C (metabolic rates decrease, and turtles become less mobile, Schwartz 1978, Witt et al. 2007a), and colder waters can thus serve as barriers for the distribution of marine turtles (Polovina et al. 2004, McMahon & Hays 2006, Hawkes et al. 2007b). The leatherback turtle is the exception, being able to maintain its body temperature well above that of the surrounding ambient water (up to 18°C higher, Bostrom & Jones 2007), and is thus capable of foraging in colder waters (10–12°C, Witt et al. 2007b). Báez et al. (2011) found increases in stranding events among Mediterranean juvenile and adult loggerheads associated with regional decreases in SST, resulting from an increasing frequency of North Atlantic Oscillation (NAO) positive phases. Atmospheric CO_2 concentrations seem to be the underlying cause of the current positive NAO index trend, creating colder and drier conditions over the Mediterranean region (Gillett et al. 2003), so despite a generalized increase in ocean SST, some regions will experience colder seawater in the future (Gillett et al. 2003). Griffin et al. (2019) found that warmer SST during autumn months surprisingly increased the risk of cold-stunning in Kemp's ridley turtles, because they dispersed further north to forage, but then retreated away from winter cold waters too slowly. Higher temperatures, on the other hand, can induce indirect stress by promoting the growth of pathogens and of toxic phytoplankton (Plotkin 2003); however, the seawater temperature corresponding to the upper thermal maximum in marine turtles is unknown, likely because such extremes are not experienced under present conditions. Yet recent research suggests that SST at inter-nesting sites in Southeast Asia will exceed the critical thermal maximum of leatherback turtles under future climate scenarios (Dudley & Porter 2014, Dudley et al. 2016). Increases in SST along post-breeding migration corridors may also increase basal metabolic rate of post-nesting females (Almpanidou et al. 2019), because they are ectothermic (Milton & Lutz 2003). However, this would likely be tempered by the ability of turtles to exploit thermally variable habitats at depth and in different water bodies (e.g. Schofield et al. 2009). Some species/populations may already be adapting to changing ocean temperatures; for example, Eastern Pacific olive ridley turtles *Lepidochelys olivacea* foraged further north during an El Niño year, avoiding warmer waters while seeking more productive upwelling areas (Plotkin 2010), while hawksbills in the Gulf of Arabia avoid warmer foraging areas during the summer months, when seawater temperatures exceed 33°C (Pilcher et al. 2014).

Sea surface currents near nesting beaches are known to facilitate the oceanic dispersal of post-hatchlings (Putman et al. 2010, Scott et al. 2014, Wildermann et al. 2017), likely influencing the ensuing spatial distribution of juveniles and their recruitment to suitable foraging grounds (Hamann et al. 2007). Yet small juveniles and even post-hatchlings are capable of oriented swimming (Putman & Mansfield 2015, Briscoe et al. 2016, Lalire & Gaspar 2019), allowing them to stay within preferred thermal conditions (Mansfield et al. 2014, 2017) and potentially to respond to some level to future changes. However, strong sea surface currents near the nesting beach and high-intensity storms may still mediate the initial dispersal of post-hatchlings (Hays et al. 2010b, Monzón-Argüello et al. 2012, Ascani et al. 2016, DuBois et al. 2020). Models have shown that patterns of dispersal are already likely highly variable because of short-term variation (Scott et al. 2017). For example, variations in sea surface current strength, associated with the Pacific Decadal Oscillation was shown to impact the dispersal of first-year loggerhead turtles in relation to a high productivity oceanic front (Ascani et al. 2016), while storms were shown to influence the dispersal of post-hatchling Atlantic loggerhead turtles (Monzón-Argüello et al. 2012), and Gulf of Mexico Kemp's ridley turtles (DuBois et al. 2020). The direction of the impacts from climate-forced dispersal is not well understood, and it is unclear whether juvenile turtles will end up in suboptimal (Monzón-Argüello et al. 2012, Ascani et al. 2016, DuBois et al. 2020), or in more favourable conditions (Ascani et al. 2016, DuBois et al. 2020). Either way, climate-forced dispersal could influence survival and thus population recruitment (Ascani et al. 2016). Notably, breeding loggerhead turtles in the Mediterranean were found to follow dispersal patterns similar to post-hatchlings, associated with prevailing currents near the nesting beach, suggesting that the initial phase of dispersal can be very important to imprint possible future foraging grounds (Hays et al. 2010b).

Multiple approaches have established our knowledge of the spatial ecology of marine turtles. Satellite tracking has become common for studying marine turtle movements (Jeffers & Godley 2016, Hays & Hawkes 2018), providing a bulk of data on their spatial distribution, connectivity, and foraging strategies. Molecular analyses have also been essential to unravel patterns of connectivity between nesting beaches and foraging areas, often coupled with ocean circulation models, allowing inferences on dispersal routes (Blumenthal et al. 2009, Putman & Naro-Maciel 2013, Putman et al. 2014). These spatial data, in combination with satellite-based environmental data, have been used to generate ecological niche models of marine turtle populations (Witt et al. 2010, Pike 2013b, Pikesley et al. 2013, Mansfield et al. 2014, Varo-Cruz et al. 2016), predicting where future suitable foraging habitats may be located in response to increasing seawater temperatures. For example, the foraging thermal niche of Atlantic leatherback turtles, and that of Atlantic and Mediterranean loggerheads, is predicted to expand northwards (Witt et al. 2010, Dudley & Porter 2014, Pikesley et al. 2015), while for Eastern Pacific leatherbacks, range contraction has been predicted (Willis-Norton et al. 2015).

Despite great technological and analytical advances, there is still need for synthetic information on the spatial distribution of marine turtles at sea at ocean scales and across life stages, to improve inferences on how they may be affected by climate change during their marine life stage. To carry out modelling to investigate this, more data on the spatiotemporal distribution of marine turtles are required. Telemetry data can provide invaluable information (but usually only describe a limited number of individuals that may not be representative of the population-level spatial distribution, Lascelles et al. 2016), and standardised surveying (Thomas et al. 2010, Buckland et al. 2015) either by boat-based or aerial distance sampling methods (Beavers & Ramsey 1998, Eguchi et al. 2007, Lauriano et al. 2011, Fuentes et al. 2015, Williams et al. 2017, Vandeperre et al. 2019) allow for in-water estimations of both population abundance and distribution (within the survey region). Additionally, both the use of unmanned aerial vehicles and underwater video (Dunstan et al. 2020) have been proposed as cost-effective alternatives to standard surveying. We suggest that the wealth of turtle tracking data that already exist, if aggregated across the decades and ocean basins over which they have been collected (Godley et al. 2008, Hays & Hawkes 2018), could go a long way to improve our understanding on the climatic drivers of spatial distribution.

Importantly, expected increases in seawater temperature will differentially affect primary production and composition of prey communities across geographic regions, with consequences for the spatiotemporal distribution of current foraging areas (Polovina et al. 2011, Poloczanska et al. 2016). Yet, estimations of future suitable habitat under climate change have broadly relied on thermal niche modelling (Witt et al. 2010, Pikesley et al. 2015, Dudley et al. 2016), while changes in hydrological processes, which will determine the magnitude and distribution of ocean productivity, and consequently the availability of prey, have been less considered. However, the strongest impacts of increases in seawater temperature may be mediated through food availability (Stubbs et al. 2020), at least for some species. In such a scenario, turtles that find prey less available may not meet summit energy reserves for reproduction and will thus have increased remigration intervals and reduced reproductive lifetime (Stubbs et al. 2020). The opposite could potentially be possible if food availability, or its quality, were increased, as this could lead to faster growth, younger age at maturity, and more frequent breeding. This may be particularly important for species or populations with specialist diets (Witt et al. 2010, Bell 2013). Ideally, estimates of future resource availability, coupled with information on foraging strategies and diet composition, would be integrated in spatial distribution forecasts. There is, however, a lack of research on marine turtle foraging habitat quality under climate change scenarios and on the potential consequences for somatic growth, limiting such integrated approaches.

4.5. Breeding patterns

Marine turtles perform cyclic migrations to breeding sites and display significant inter-population variability in the start and duration of nesting seasons (Miller 1997). Body condition determines when breeding can occur (Miller 1997, Broderick et al. 2001b), and is likely driven by resources at foraging areas which, in turn, may depend on mid- to long-term environmental conditions (Limpus & Nicholls 2000). For example, cooler waters have been shown to enhance food availability for loggerheads in the Pacific, boosting their breeding capacity (Chaloupka et al. 2008). The precise timing of nesting may depend on short-term environmental cues, such as seawater temperature (Weishampel et al. 2004, Pike et al. 2006, Hawkes et al. 2007a, Mazaris et al. 2008). Understanding how climate variables impact the breeding phenology of marine turtles is crucial, as changes in the timings of migration, courtship, and the onset and duration of nesting can exacerbate or reduce climate change impacts on the nesting beach (Pike et al. 2006, Mazaris et al. 2008, Pike 2009, Weishampel et al. 2010, Patel et al. 2016).

With the increase in research looking at phenological responses to global warming, 2 things have become clear: there are both inter- and intra-specific differences in responses, and it is not straightforward where to look for environmental drivers of breeding cycles. While previous research has focussed on environmental conditions near the nesting beach, recent work indicates that conditions at distant foraging grounds are more likely to influence the timing of migration and arrival at the breeding area for the start of courtship and nesting (Mazaris et al. 2009b, Neeman et al. 2015a, Monsinjon et al. 2019b). It is intuitive that the onset of the breeding migration is triggered by environmental conditions experienced at foraging areas (provided that suitable energetic conditions for reproduction are met), yet, once near breeding sites, where females and males aggregate for courtship and mating (Limpus 1993, Fitzsimmons et al. 1995, Arendt et al. 2012), the local seawater temperature seems to influence the timing of nesting, potentially because temperatures regulate the rate of egg maturation (Weber et al. 2011, Valverde-Cantillo et al. 2019). Thus far, loggerhead turtle populations have consistently been found to begin nesting earlier in response to higher annual SST, both near the nesting beach (Weishampel et al. 2004, 2010, Pike et al. 2006, Hawkes et al. 2007a, Mazaris et al. 2008, 2013, Lamont & Fujisaki 2014, Patel et al. 2016), and at foraging sites (Mazaris et a. 2009b, Monsinjon et al. 2019b), albeit at different rates (Mazaris et al. 2013). Among green turtles, however, except for 1 study (Weishampel et al. 2010), no phenological changes in response to inter-annual SST near breeding sites (Pike 2009, Dalleau et al. 2012), or at foraging areas (Valverde-Cantillo et al. 2019) have been reported, and at least 1 population of leatherback turtles has demonstrated delayed onset of nesting following warmer SST at foraging areas (Neeman et al. 2015a).

Some studies have also reported a correlation between higher SST and fewer clutches (Mazaris et al. 2009b, Reina et al. 2009, Patel et al. 2016), likely as a result of fewer turtles nesting. These observations could indicate an indirect effect of seawater temperature on the availability of food resources at foraging habitats (Chaloupka et al. 2008, Neeman et al. 2015a), leading to delays in the build-up of energy reserves for reproduction (Neeman et al. 2015b, Stubbs et al. 2020). Another study found that more clutches were laid at a green turtle rookery following warmer SST during the winter prior to the nesting season (Bruno et al. 2020). As seawater temperature is likely to impact different trophic levels in different ways, depending on their prey, marine turtle populations may be differentially affected. It is also possible that increases to seawater temperature will enhance food resources for turtles particularly at higher latitudes, near the current limits of their distribution or beyond. Increases in re-migration intervals due to slower build-up of energy reserves can lead to shorter nesting seasons (Robinson et al. 2014), presumably because fewer females undertake the breeding migration (Limpus & Nicholls 2000, Neeman et al. 2015a). Conversely, nesting years with more turtles breeding lead to longer nesting seasons (Pike 2009). In fact, the size of the nesting population can be a predictor of both nesting season onset (Robinson et al. 2014) and length (Monsinjon et al. 2019b). However, because higher SST can reduce inter-nesting intervals, likely by enhancing metabolic rates and the rate of oogenesis (Weber et al. 2011, Valverde-Cantillo et al. 2019), during a warm year, the same number of clutches could be laid in a shorter period (Pike et al. 2006). Results thus far are not conclusive, as both longer (Weishampel et al. 2010, Lamont & Fujisaki 2014) and shorter nesting seasons (Pike 2009, Weishampel et al. 2010) have been observed in warmer years. Geography may account for some of the observed discrepancies, as latitudinal variation in phenological responses to SST have been observed among loggerheads, with the response of poleward populations being stronger (i.e. greater adjustment in the nesting date, Mazaris et al. 2013). Closer to the equator, on the other hand, likely due to a wider temporal range of suitable thermal conditions, populations show less sensitivity to increases in SST (Mazaris et al. 2013), or perhaps they are harder to detect. A latitudinal gradient (associated with an SST gradient) in the onset of nesting has also been observed among green turtles (Dalleau et al. 2012).

The onset and duration of the nesting season may also depend on age, as remigrant turtles tend to begin nesting earlier and lay more clutches than neophytes (Rafferty et al. 2011, Stokes et al. 2014). It is thus clear that breeding phenology depends on a diverse suite of factors, including resource availability, resource acquisition, environmental cues at both foraging and breeding sites, courtship, population demography (i.e. abundance and age of nesting females) and geography, and this complexity needs to be taken into consideration in future assessments. On the other hand, understanding the dynamic responses of breeding turtles to environmental conditions is critical to interpret the inter-annual variability in clutch numbers, and to improve estimates of population trends based on nesting data (Neeman et al. 2015a).

To date, few studies have assessed whether phenological changes by marine turtles in response to climate change will be sufficient to maintain suitable incubation conditions (Patel et al. 2016, Almpanidou et al. 2018, Monsinjon et al. 2019a). At higher latitudes, earlier nesting may track current nesting thermal conditions (Patel et al. 2016, Almpanidou et al. 2018, Monsinjon et al. 2019a), although this effect may be temporary (Patel et al. 2016), and dependent on the severity of future climatic change (Monsinjon et al. 2019a). On the other hand, Monsinjon et al. (2019a) estimated that under an optimistic climate warming scenario, 6 out of 7 loggerhead populations may not be able to cope with the impacts of climate warming on hatching success and primary sex ratio by adjusting their breeding phenology. A different study suggested that loggerhead turtles may not be able to track current precipitation conditions (Almpanidou et al. 2018), known to also impact hatching success (Santidrián Tomillo et al. 2015b, Montero et al. 2018a) and primary sex ratio (Lolavar & Wyneken 2017, 2020).

Geographic and species disparities persist in the available research on the impacts of climate change on the breeding patterns of marine turtles, which limits generalized assumptions. There is thought to be a genetic basis to the plasticity of breeding phenology (Visser et al. 2010), but this remains to be thoroughly investigated for marine turtles. Some studies have tested this hypothesis using mitochondrial DNA control region haplotypes (Dalleau et al. 2012, Mazaris et al. 2013), which trace the dispersal of female lineages, and are the most commonly used markers in marine turtle population genetics research (Bowen & Karl 2007, Tikochinski et al. 2018). However, this marker represents a very small portion of the genome, greatly limiting the chances to detect variability. Recent advances in next-generation sequencing provide reliable and relatively low-cost genomic data, which coupled with new analytical approaches allow genome-wide association studies to detect polymorphisms that are associated with observed inter-population differences in a trait, such as phenology (Visser et al. 2010, Ahrens et al. 2018). We also have yet to investigate how climate change may impact courtship behaviour and mating success (which is particularly difficult because the information on breeding males is very limited) and what may be the advantages of seasonal versus bimodal versus all-year nesting and the drivers of these different breeding patterns.

In addition, there is a lack of standard metrics to define breeding phenology parameters (e.g. the start and duration of the nesting season), making comparisons between studies almost impossible. Some applied metrics include 'median nesting date' (Pike 2009, Weishampel et al. 2010, Lamont & Fujisaki 2014, Robinson et al. 2014), 'date of first nest' (Mazaris et al. 2009b, 2013), and 'peak nesting period' (Dalleau et al. 2012). We suggest that using first nesting event can be problematic, as this reflects atypical events (outliers). Thus, for populations with nesting seasons delimited in time, we recommend using the 2.5th percentile of nesting date as a proxy for the beginning of nesting, to avoid outlying data. Using the median nesting date can also be ambiguous, as this metric is influenced both by the onset and by the duration of the nesting season (Mazaris et al. 2013) and survey effort. Furthermore, several populations have bimodal or year-round nesting (Dalleau et al. 2012), making most of these metrics impractical. Future studies could benefit from models based on a biologically meaningful description of nesting phenology dynamics, which can accommodate missing data (e.g. due to uneven monitoring effort or to very high nesting density, Girondot 2010, 2017, Laloë et al. 2020) that are freely available (R package 'phenology'; Girondot 2020b).

4.6. Nesting area availability

The area available for marine turtles to nest is likely to be reduced by sea level rise (SLR, Fish et al. 2005, Baker et al. 2006, Fuentes et al. 2010b), with beaches in developed regions being likely the most vulnerable, since coastal development can prevent the natural movement of sediment, causing coastal squeeze and exacerbating impacts from SLR (Fish et al. 2008, Mazaris et al. 2009a, Biddiscombe et al. 2020). Reductions in available nesting area may also amplify density-dependent issues at marine turtle nesting beaches (e.g. risk of infection in clutches and accidental destruction of eggs by nesting females), and create suboptimal nesting habitats (Girondot et al. 2002, Tiwari et al. 2010). SLR may also increase exposure of clutches to saltwater inundation, ultimately affecting hatching success and hatchling fitness (Patino-Martinez et al. 2014, Pike et al. 2015). Storms (tropical storms, hurricanes, cyclones, or typhoons) can cause further impacts on marine turtle nesting beaches and their reproductive output, with storm frequency and intensity expected to increase in future warmer environments (Webster 2005, Van Houtan & Bass 2007, Fuentes & Abbs 2010, Fuentes et al. 2011a, Long et al. 2011).

Despite the potential impacts of SLR and storms on marine turtle nesting grounds and their reproductive output, only a few studies have projected how these climatic processes will impact marine turtles. This is likely a reflection of the challenges inherent in successfully predicting shoreline response to SLR and storm activities (Cooper & Pilkey 2004, Von Holle et al. 2019), and the inability to couple projections with biological information (e.g. nest site choice, responses to changes in beach morphology). Most of the studies to date (e.g. Baker et al. 2006, Mazaris et al. 2009a, Fuentes et al. 2010b, Reece et al. 2013, Varela et al. 2019, Veelenturf et al. 2020) have used the Bruun rule or 'bathtub' models to determine the potential loss of marine turtle nesting beaches to various scenarios of SLR. However, these approaches do not account for natural beach movement and sand transport, and consequent changes in beach profiles (Cooper & Pilkey 2004, Woodroffe 2008), although some studies have considered the extent to which nesting areas may shift in relation to natural and artificial physical barriers (Fish et al. 2008, Katselidis et al. 2014, Biddiscombe et al. 2020, Lyons et al. 2020). These assessments have often been coupled with data from field survey methods (e.g. beach profiles, using Emory or Abney Level methods; see Fish et al. 2005, 2008), which tend to be limited to discrete beach transects and are subject to systematic errors and low accuracy (Isaak et al. 1999), or from terrestrial and airborne light detection and ranging (LiDAR, Long et al. 2011, Yamamoto et al. 2015), which has higher accuracy, as well as cost (Varela et al. 2019). To offset some of the issues from traditional approaches, a novel combination of drone-based photogrammetry and a low-cost and portable real-time kinematic GPS has been suggested to develop the digital terrain models needed to assess the impacts of SLR on marine turtle nesting grounds (Varela et al. 2019).

Recent studies (Butt et al. 2016, Von Holle et al. 2019, Lyons et al. 2020) have taken advantage of other novel sophisticated approaches (e.g. coastal vulnerability index, storm surge models, SLR calculators) and open-access geomorphology datasets (e.g. LiDAR, digital elevation models) combined with turtle nest location data to assess the impacts of SLR on rookeries. However, these are generally developed for broad-scale assessments (e.g. continental, global); therefore, finer-scale analyses are necessary to improve current assessments of the impacts of SLR on marine turtles. Process-based models (e.g. Delft3D and XBeach) can directly simulate beach hydrodynamics and sediment transport, and provide more robust assessments of the potential impacts of SLR on marine turtle nesting areas. For example, these models account for non-erodible portions of the beach (due to shoreline protection strategies such as sea walls, groynes, and other hard sea defences), which will become more prevalent as sea level rises and storms become more frequent, and evaluate how current or proposed installation of these interventions could alter the risk of habitat loss under various scenarios of SLR and storm activity, which remains a big gap in our knowledge.

In addition to the uncertainty in how SLR/storms will affect specific nesting beaches, there is still considerable uncertainty on how marine turtles will respond to changes in beach profiles, and the availability of nesting areas as well as the effects of synergistic and cumulative impacts from other climatic pressures (e.g. temperature, rainfall, Fuentes et al. 2011a). The threat of SLR/storms coupled with contemporary anthropogenic threats (e.g. coastal development or pollution), may weaken the ability of marine turtles to cope with climate change (Reece et al. 2013, Fuentes et al. 2016a, Biddiscombe et al. 2020, Fuentes et al. 2020). While marine turtles can buffer effects from individual storm events, by laying multiple clutches spaced throughout the nesting season (Dewald & Pike 2014, Fuentes et al. 2019), climate change scenarios suggest that this threat will become of greater concern in the future (Fuentes & Abbs 2010, Fuentes et al. 2019). Therefore, there is a need to understand the magnitude of the potential impact from storms at a rookery level (e.g. loss of eggs and habitat) and across populations. Some studies have looked at the exposure of marine turtle nesting beaches to storms (Fuentes et al. 2011a, 2019, Dewald & Pike 2014), but these do not usually quantify the actual loss in turtle reproductive output, or they focus on single nesting beaches (for examples, see Foley et al. 2006, Caut et al. 2010, Long et al. 2011, Ehrhart et al. 2014). Future research should focus on the long-term impact of storms and implications at a population level. Such assessments would benefit from improvements in our understanding of how well eggs can withstand inundation. Recent studies have found that short periods of inundation (1–6 h) did not significantly reduce hatching success (Pike et al. 2015, Limpus et al. 2020), and that embryos may be more vulnerable at the beginning and at the end of development (Limpus et al. 2020). Tolerance thresholds could then be integrated with inundation models, such as wave run-up models, to better identify areas at significant risk of wave exposure from SLR/storms (Ware et al. 2019).

As nesting beaches become unsuitable or unavailable, marine turtles may respond by shifting their range to climatically suitable areas (Hamann et al. 2013, Abella Perez et al. 2016, Mainwaring et al. 2017). Some studies also suggest that marine turtles may respond to changes in beach profiles (due to SLR/storms) through nest-site selection, as some populations seem to favour elevated sites for nesting, increasing clutch survival (Santos et al. 2017, Patrício et al. 2018). To date, only a few studies have explored potential range shifts as suitability of nesting beaches changes, and predicted that some populations may be able to shift their nesting distribution as climate change progresses (McMahon & Hays 2006, Pike 2013a, Butt et al. 2016, Fuentes et al. 2020). Newly colonized areas must provide the necessary conditions for egg incubation (Katselidis et al. 2012) and hatchling dispersal, but other factors will influence the potential for rookery establishment, such as the presence of other hazards.

This is important because range shifts may result in increased exposure to anthropogenic threats, such as coastal development (Pike 2013a, Biddiscombe et al. 2020, Fuentes et al. 2020). Our current lack of understanding of the synergistic effects of multiple climatic processes with other anthropogenic factors hinders our ability to identify suitable areas that will allow turtle nesting to persist (Fuentes et al. 2013). Thus, a future emphasis should be on coupling predicted range shift studies with assessments of exposure to threats with considerations to the interconnected nature of impacts and responses for a multitude of processes.

4.7. Emerging diseases and pathogens

Infectious disease outbreaks have increased in some marine taxa in the last few decades (e.g. Fisher et al. 2012, Altizer et al. 2013, Sanderson & Alexander 2020), potentially driven by either climatic or anthropogenic factors, but likely by a combination of both (Fey et al. 2015). It is clear that stressors such as these exacerbate the impact of disease (Hing et al. 2016) and that climate change, particularly warming temperatures, ocean acidification, changes in precipitation, and storm damage, may alter marine disease dynamics (Harvell et al. 2009, Tracy et al. 2019). To date there is no clear evidence of recent increases in marine turtle diseases (Tracy et al. 2019), but this may also be due to a lack of baselines, and/or limited research in this field (Tracy et al. 2019).

One of the major diseases of marine turtles is fibropapillomatosis (FP), a neoplastic disease characterized by external and internal tumours, which affects all 7 species, and is reported globally (Jones et al. 2016). FP tumours, if sufficiently numerous and large, can impede sight, swimming, feeding, and breathing, and can suppress organ function, leading to death (Herbst 1994). FP is linked to infection by a herpesvirus, the chelonid herpesvirus 5 (ChHV5, Patrício et al. 2012, Alfaro-Núñez et al. 2014, Page-Karjian et al. 2015); however, the virus transmission route is not clear, and environmental factors may also play a role in disease expression (Van Houtan et al. 2010). Although widespread, FP currently does not seem to pose a major threat to marine turtles (Patrício et al. 2016), but if warmer seawater were to promote tumour growth (which remains to be empirically demonstrated, but appears possible; Herbst 1994, 1995, Foley et al. 2005), outbreaks could increase in severity in the future.

The prevalence of fungal infectious diseases has increased in marine turtles in recent decades (Phillott & Parmenter 2001, Fisher et al. 2012, Gleason et al. 2020), with a newly emerging fungal disease reported worldwide to affect marine turtle clutches, the ‘sea turtle egg fusariosis’ (STEF, Gleason et al. 2020). It appears to be caused by the *Fusarium solani* species complex, a group of at least 26 common soil fungi that colonize plant materials in the division Ascomycota (Short et al. 2013), 2 of which have been shown to be particularly virulent, *F. falciforme* and *F. keratoplasticum* (Sarmiento-Ramírez et al. 2014). The fusarium species infect incubating eggs, creating yellowish-blue infection zones that become necrotic, eventually leading to embryo death (Gleason et al. 2020). Pathogenic fusarium species have also been isolated from healthy eggs, indicating that they may be normally present, but unremarkable unless stressors weaken the host immune system (Sarmiento-Ramírez et al. 2014). Notably, tidal inundation was shown to correlate with STEF prevalence, leading to higher clutch mortality (Sarmiento-Ramírez et al. 2014), implying that future SLR and storm surges may influence disease spread. Additionally, future loss of nesting area may increase nest density (Patrício et al. 2019), favouring pathogen spread among neighbouring clutches (Sarmiento-Ramírez et al. 2017).

Climate change can also alter host–pathogen interactions, either by impairing host immune systems or by altering the virulence of pathogens, and this has been documented in shellfish, coral, and some fish species (Burge et al. 2014), but not yet in marine turtles. Warming seas may also allow pathogens to increase their range, while simultaneously, poleward shifts in host species range in response to climate change may bring them into more frequent contact with known or novel pathogens (Cohen et al. 2018). Marine diseases may also impact foraging habitats on which marine turtles depend, for example seagrass meadows (Sullivan et al. 2018) and coral reefs (Precht et al. 2016, Tracy et al. 2019), but much work remains to demonstrate how and at what magnitude climate change may impact these habitats, and determine what capacity marine turtles have to broaden their diets. Future research should focus on understanding which environmental factors favour the colonization and infection of clutches by pathogenic fungal species, and which factors promote FP tumour growth. Disease monitoring using standard operational protocols should also be encouraged to improve baselines, essential to detect change, under future climatic conditions.

5. STRATEGIES TO REDUCE CLIMATE CHANGE IMPACTS

Faced with the certainty of future climate change, it seems logical that strategies to reduce the potential negative impacts of climate change on marine turtles should be investigated. Here we distinguish ‘intervention’, which we define as the direct manipulation of the ecological processes of turtles, and ‘mitigation’, which is the reduction of stressors on marine turtles in order to give them the best possible opportunity to adapt by themselves. Interventions that have been proposed so far include relocating nests to hatcheries or artificial incubators, and manipulating incubation temperatures using shade, water sprinklers, native vegetation, or the addition of sediment with different colour (and therefore albedo) and grain sizes (Table 1; Kamel & Mrosovsky 2006, van de Merwe et al. 2006, Fuentes & Cinner 2010, Fuentes et al. 2012, 2016b, Patino-Martinez et al. 2014, Wood et al. 2014, Hill et al. 2015, Jourdan & Fuentes 2015, Liles et al. 2019). Mitigations that have been proposed include identifying and legally protecting extant and future suitable nesting beaches (e.g. male-producing beaches and/or areas with low risk of inundation and erosion; Baptistotte et al. 1999, dei Marcovaldi et al. 2016), establishing marine protected areas (MPAs) to protect both dynamic habitats (i.e. habitats that may change in space and/or time) and the marine turtles that occupy them (Maxwell et al. 2020), as well as mitigating other anthropogenic stressors (Fuentes et al. 2013).

It seems sensible to suggest that mitigation activities can and should be used widely to help reduce the impact of climate change and other stressors to marine turtles. However, whether any interventions would be helpful or wise to employ is still influenced by our understanding of their associated effectiveness, feasibility, and risks (see summary Table 2 in Fuentes et al. 2012, Jourdan & Fuentes 2015). For example, to assess the utility of interventions related to changes in sex ratio, ideally we should know what primary sex ratio and OSR would be ‘optimal’ in the population that we are managing, and the resulting consequences of manipulating sex ratio on population dynamics and evolutionary potential (Fuentes et al. 2012). On the one hand, if too few males are produced for the population to remain fertile, it risks becoming extirpated (see Section 2.1). On the other hand, if we assume that the survivorship between male and females is equal, if the proportion of females is reduced in lieu of manipulation for males, the population growth rate might slow, because the finite rate of population increase is set by the proportion of females (Boyle et al. 2014a), which can eventually reduce the capacity of the population to adapt. Thus, manipulation of primary sex ratios may be risky, and lacks an adequate knowledge base at present to be widely, safely implemented (Santidrián Tomillo & Spotila 2020). Similarly, to determine the need for interventions to address impacts from nest inundation and wash-over associated with rises in precipitation, sea level, and storm activities, we need to be able to predict the spatiotemporal threat of inundation/washover at individual beaches and the consequent risk to incubating eggs, based on embryonic tolerances (Ware et al. 2019). This information must be weighed against information on the risks of intervening (e.g. relocating, Ware & Fuentes 2018).

Direct strategies may become necessary at some sites, as the negative effects of climate change become more extreme (Prober et al. 2019). For this, decisions will need to be made at a site level and with consideration of the environmental, social, economic, and cultural conditions of specific locations (Fuentes et al. 2012). As intervention strategies are trialled, it is critical that information about their effectiveness is documented, so that managers at other sites can learn, and an adaptive management approach can be taken (Fuentes et al. 2016b). Importantly, any approach should be based on our best understanding of the population level impacts of, for example, manipulating sex ratio, and consider the long-term (e.g. >100 yr) persistence of marine turtles. This should also be set against the risk of creating ‘maladapted’ phenotypes and altering the gene pool by carrying out inappropriate intervention (see Mrosovsky 2006). Thus, it is suggested that we should not intervene with incubating clutches until we know what the consequences are, and instead we should prioritize the protection of areas that will have climatically suitable conditions for incubation over the long-term and that will have reduced impact by SLR (Fuentes et al. 2020), including minor rookeries, especially if they have male-producing conditions (dei Marcovaldi et al. 2016). As climate change progresses and temperatures become extreme, causing high mortality rates and low production, there might be a shift in management goal from obtaining OSRs versus preserving hatching productivity. However, if the vast majority of eggs are failing due to habitat conditions (e.g. low beach profile leading to inundation of clutches, or extremely high incubation temperatures), it might indicate that a beach is probably no longer suitable for incubation, so the efficacy of increasing the production of hatchlings that might

Table 1. Potential strategies to mitigate the direct impacts of climate change on marine turtles, and knowledge gaps in relation to the effectiveness, and ecological risks of implementing strategies. Information presented in the last two columns was adapted from Fuentes et al. (2012)

Metric	Impacted life stages	Observed and projected impacts	Climatic drivers	Strategies to reduce climate change impacts	Knowledge gaps
(1) Sex ratio	- Hatchlings	- Change in sex ratio - Destabilization of population dynamics - Reduction of effective population sizes	- Increases in air and sea surface temperatures - Altered rainfall and humidity regimes - Sea level rise - Extreme weather events (cyclones and floods)	- Prevent removal of beach vegetation - Re-vegetation or planting native vegetation - Identify and legally protect beaches that have climatically suitable environment and/or produce higher proportions of male hatchlings - Manipulate incubation temperature *in situ* using water sprinklers, shade, or by adding lighter sediment to the beach - Move nests to areas with suitable conditions, hatcheries, or incubators	- Current hatchling sex ratios at key nesting beaches, and intra-beach variability in these ratios - Pivotal temperature and upper thermal threshold for each sea turtle species and for key populations - Level of plasticity and heritability in temperature-dependent sex determination - Optimal primary and operational sex ratios for each sea turtle species and for key populations - How much sex ratios should be manipulated to maintain optimal sex ratio - Optimal incubation environments for successful hatching for different species - Effects of cooling nests with sprinklers on rates of fungal infection - Impact of different manipulating interventions on nest temperature, and how this varies spatially and temporally at key nesting sites - Effects of watering on the temperature and moisture of the nesting environment and whether this affects sex ratios and hatching success - Thermal properties of different sediments and how they affect hatching success and sex ratios - Amount of sand, colours, and grain sizes required to change the thermal profile of nesting beaches
(2) & (3) Hatching success & hatchling condition	- Eggs - Hatchlings	- Changes in hatchling morphology, physiology, and performance - Low hatching success / failure			
(4) Movements and distribution at sea	- Hatchlings - Juveniles - Sub-adults - Adults	- Changes in hatchling dispersal - Changes in recruitment of juveniles to foraging sites - Changes in adult foraging and nesting distribution - Decrease in survival and population recruitment - Changes to the spatio-temporal distribution of foraging areas - Changes in abundance or location of food	- Changes in sea surface temperature - Changes in wind and ocean circulation - Changes in ocean stratification - Ocean acidification	Marine protected areas (dynamic, seasonal or permanent)	- Optimal design for marine protected areas (MPAs) to protect marine turtles across different life stages and under a changing climate - Effectiveness of MPAs in reducing the impacts of climate change

Table 1 (continued)

(5) Breeding patterns	- Eggs - Hatchlings - Nesting females	- Changes in the timings of migration, courtship, onset and duration of nesting - Changes in nesting intervals and reproductive output		- Assure that protection measures in place (e.g. fishing closure periods) are synchronized with the timing of aggregation of marine turtles near the nesting beach - Adapt management of nesting grounds to align with changes in nesting phenology	- Whether changes in breeding patters can ameliorate impacts of climate change - Direction of changes in breeding patterns
(6) Nesting beach availability	- Eggs - Hatchlings - Nesting females	- Loss of nesting beach - Amplification of density-dependent issues (i.e. Allee effect) - Suboptimal nesting habitats, with increased risk of inundation - Distributional shifts	- Sea level rise - Extreme weather events (cyclones and floods)	- Establish rolling easements (voluntary agreement limiting amount/type of development on property) - Incorporate climate change into land-use planning - Establish or enforce existing setback regulations - Ban and remove permanent shoreline-hardening structures - Plan urban growth to redirect development away from nesting areas - Beach replenishment - Use hard engineering structures - Install offshore breakwaters	- Ability of shorelines to respond to sea level rise and storm activities - Sediment transportation within a nesting beach with climate change - Risks associated with hard and soft engineering structures to prevent beach movement and erosion - Effects of hard and soft engineering structures on the natural morphological shift of nesting beaches and their response to sea level rise and storm activity

return to a 'doomed' beach should be evaluated. Persistence of suitable nesting habitat is crucial for the reproduction of marine turtles and is one of the key factors influencing the resilience of marine turtles to climatic changes (Fuentes et al. 2013).

Although substantial knowledge gaps remain to efficiently manage climate-change-related threats to incubating eggs, larger knowledge gaps remain in relation to turtles at sea (Table 1). Large and mobile MPAs have been suggested to protect dynamic habitats and the migratory marine species that occupy them, such as marine turtles, as climate change progresses (Davies et al. 2017, Maxwell et al. 2020). However, design of such protected areas relies on robust modelling of how marine turtles might respond to change, and whether MPAs would be effective in reducing the impacts from climate change (Lawler et al. 2010, Fuentes et al. 2012, 2016b). Until we address some of these uncertainties, we suggest focussing on enhancing marine turtle resilience by reducing other threats that they currently face (Robinson et al. 2009, Witt et al. 2010, Fuentes et al. 2013, Reece et al. 2013). The main challenge will be to account for the cumulative and synergistic nature of climate-related impacts and existing threats to marine turtles (Fuentes et al. 2011b, Reece et al. 2013).

6. RESEARCH PRIORITIES

Based on the knowledge gaps identified in Section 4, key research questions were formulated and are summarized in Box 1. Here we highlight what we see as the key priorities that urgently need to be addressed and provide suggestions where research might be best applied.

6.1. Understanding sex ratios under climate change and associated impacts

Despite decades of meaningful research, many of the current estimates of primary sex ratios may not accurately reflect the reality, given that most studies have not taken into account the large variability of natural environments throughout the full duration of nesting seasons or have used proxies with inherent limitations or do not adequately cover the beaches used by the population. What the primary sex ratios will be in the future, and how they will vary between species, rookeries, and individuals, are key questions to understand the resilience of marine turtles to climate change, which remain largely unanswered. We

Box 1. Priority research questions to improve our understanding of how climate change will impact marine turtles, for each parameter expected to be impacted, and for strategies to reduce the impact of climate change

Nest area availability
How will nesting turtles respond to changing beach profiles and inundation of current nesting areas?
What are the synergetic impacts of shoreline protection strategies and sea level rise to nesting areas?
What are the long-term impacts of more frequent and intense storm activity?
What areas will be available for marine turtles as climate change progresses?
Will adaptive shifts in nesting location lead to changes in other threats?

Sex ratios
What is the variability in temperature-dependent sex determination reaction norms between individuals, rookeries, and species?
What is the role of nest humidity in determining sex ratio?
How can models used to reconstruct nest temperature be improved?
How can we better predict beach microclimates?
What spatial and temporal scales are relevant to predict incubation temperature?
How do seasonal primary sex ratios translate into adult sex ratios?
How many males are needed to sustain populations? Is there evidence of male limitation?
What are the long-term consequences of skewed sex ratios on population dynamics and genetics?

Hatching success
Why do clutches fail at high temperatures?
What is the impact of the oxygen–temperature interaction on clutch success?
What is the lethal upper thermal limit for marine turtle clutches?
Why does the lethal upper thermal limit vary between species and populations?
Can the lethal critical thermal limit of embryos change as a result of natural selection?
How tolerant are marine turtle eggs to inundation?

Hatchling morphology, survival, and performance (hatchling condition)
Is the effect of incubation temperatures on hatchling locomotion meaningful to survival?
Do larger hatchlings from cooler incubation conditions have a reduced individual chance of predation?
How does the muscle phenotype of hatchlings vary with incubation temperature?

Movements and distribution at sea
What will be the impact of climate change on hydrological processes?
How will climate change impact foraging grounds?
How will climate-forced dispersal influence recruitment to juvenile/adult foraging grounds?
Will adaptive shifts in foraging location lead to changes in other threats?

Breeding patterns
How does latitude/local climate relate to phenological responses to climate change?
What are the drivers of seasonal, bimodal, and year-round nesting strategies?
How is courtship timing and duration affected by climate factors?
Will phenological changes be sufficient to maintain suitable incubation conditions?
Is there a genetic basis for phenological behaviour?

Emerging diseases and pathogens
Are diseases/infections of marine turtles increasing due to climate change?
Does fibropapillomatosis prevalence/severity increase with temperature?
What climate conditions favour the survival of egg fungal pathogens?

Strategies to reduce climate change impacts
What are the effectiveness, feasibility of implementation, and ecological risks associated with strategies to reduce impacts from climate change?

thus recommend a re-estimation of primary sex ratios globally, using improved metrics, sampling design, and modelling approaches (see Section 2.1), and a continuation of research on non-lethal sexing techniques (Tezak et al. 2020a). The effect of humidity on primary sex ratios also deserves more attention, particularly to clarify if there is a direct effect of water uptake on the regulation of sex-determining genes or if, otherwise, this is an indirect effect of evaporative cooling. Of extreme importance is to determine what the demographic consequences of extremely female-skewed primary sex ratios are, i.e. how these translate into OSRs. Is population growth to be expected in the short-term and collapse in the long-term? This will be fundamental to inform intervention strategies, namely if management of incubation environments is necessary, and if so, under what conditions. Another priority is to investigate to which extent male abundance limits female fecundity (Boyle et al. 2014a) and the importance of timed courtship. While male turtles are much less tractable to study (i.e. they never come ashore), given their wide-scale distribution, indirect approaches can be immediately applied, such as estimating the proportion of infertile eggs within clutches (as a proxy for fertilisation success; Phillott & Godfrey 2020) combined with genetic assessments of effective sex ratios (Lasala et al. 2018). Notwithstanding, the lack of information on this demographic group (adult males) must be addressed, particularly given their role for population persistence under future climate change. For this purpose, the Global Male Sea Turtle Initiative was created, to promote the study of male marine turtles worldwide (García-Cruz et al. 2018).

6.2. Understanding climate change impacts on embryo and hatchling survival

Severe weather conditions (extreme high incubation temperatures, storm surges, and protracted inundation), are often predicted to cause clutch mass mortality; however, the lethal upper thermal limits of some species are yet to be estimated, and the tolerance of marine turtle clutches has rarely been studied (but see Pike et al. 2015 and Limpus et al. 2020). Reports on these parameters are essential, assessing variability between species and populations and the influence of environmental factors (e.g. clutch size, nest depth, and sediment type). More consideration should be given to the role of the oxygen–temperature interaction on the thermal tolerance of embryos and on hatchling muscle performance (Liang et al. 2015, Booth 2017, Stubbs & Mitchell 2018), as a warmer climate may simultaneously increase oxygen consumption rates, while contributing to oxygen depletion (e.g. due to SLR/storm-related inundation or to metabolic activity of nearby eggs at high nest density sites). Additionally, improved models of beach sediment movement in response to SLR are critical for robust estimations of clutch flooding/nesting area loss. The information relative to the impacts of diseases and pathogens is also scarce, and despite the increase in fungal infections among incubating clutches, there is a lack of baselines precluding the estimation of change under future conditions, and more importantly, there is no clear understanding of how pathogens will respond under a warmer climate. There is likewise a need for research on the downstream consequences of the incubation environment on hatchlings; particularly, it is critical to discern if body size has an impact on the relative predation risk, and if the amount of yolk reserves is important for dispersal and survivorship.

6.3. Assessing the potential for adaptation

Understanding the capacity for physiological adaptation to future climate change is a major priority; specifically, studies should assess the plausibility for adaptation of critical thermal limits of incubation through natural selection, suggested by plasticity in the expression of genes that mitigate cell damage under heat stress (heat-shock genes, Tedeschi et al. 2016). Possibly, however, marine turtles will respond more rapidly to adverse climatic conditions by shifting their spatiotemporal distribution and/or changing their nesting/foraging behaviour, but there is still limited information on their expected responses to climate change, and even more so, on the efficacy of such responses (Fuentes et al. 2020). Future research should thus assess how nesting females and foraging animals respond to climate-related changes, such as rising sand temperatures, altered beach profiles, inundation of current nesting areas, and increasing seawater temperatures, taking into account site-specific sensitivities (e.g. Dalleau et al. 2012, Mazaris et al. 2013). Genome-wide association studies will also be key to assess if relevant behaviours (e.g. nest-site choice, phenological responses to temperature) have a genetic basis, and are thus susceptible to evolution by natural selection. Perhaps even more important will be to quantify the efficiency of potential (and observed) responses to climate change. For instance, will marine turtles shift their distributions to areas where anthropogenic disturbance is high (Fuentes et al. 2020)? Will phenological changes be sufficient to maintain suitable incubation conditions (Monsinjon et al. 2019a)? Answering these questions will be critical to anticipate the need for mitigation strategies. Lastly, a key action is to identify (and legally protect) beaches that will become (or remain) suitable for nesting under climate change. This may imply surveying beaches with current very little to no nesting, yet it may be the single most important strategy to enhance the resilience of these animals in the long-term.

6.4. Understanding climate change impacts on foraging ecology

The lack of information regarding the impacts of climate change on foraging grounds and the interactions between food availability and the somatic growth of marine turtles is a considerable obstacle to predicting the responses of marine turtles to future conditions. Somatic growth is a key demographic parameter, as it will impact the age at maturity, and thus the reproductive output of populations. Decreases in somatic growth among Pacific green turtle foraging aggregations have been associated with an El Niño event, leading to cooler SST and lower net productivity (Chaloupka et al. 2004). In the Western Atlantic, on the other hand, declining somatic growth rates across multiple foraging grounds and 3 marine turtle species (green turtles, hawksbills, and loggerheads), occupying different trophic positions, have been associated with warming SST (Bjorndal et al. 2013, 2016, 2017), and the authors suggested that indirect effects of the seawater temperature on net productivity may be driving these declines. Recent research has further highlighted that food limitation due to climate change is likely to have the strongest impact on population persistence among herbivorous green turtle populations (Stubbs et al. 2020), but more research is needed, encompassing more populations and wider geographic scales. The additional layers of trophic complexity for carnivorous and omnivorous species like ridley, flatback *Natator depressus* and loggerhead turtles may make such modelling efforts more difficult. It is fundamental to assess how the distribution and abundance of food resources will change under future climate scenarios. For instance, some seagrass species are predicted to decline with increases in seawater temperatures (Jordà et al. 2012), but there is insufficient information to make predictions at a global level (Unsworth et al. 2019). Some food resources may become more abundant under future climate change (Bell et al. 2013), which, coupled with faster metabolism, could increase food intake and enhance growth rates, and lead to lower age at maturity and thus to longer reproductive periods and higher breeding rates. We need basic knowledge on how climate change will impact hydrological processes, such as ocean circulation and mixing, turbidity, upwelling regimes, water column stratification, and the distribution of frontal and convergence zones, as these processes, combined with changes in SSTs and in water acidity, will affect ocean productivity and consequently, the availability of food for marine turtles. This type of assessment will benefit from collaborations between transdisciplinary research teams. It is also essential to study the diet and foraging plasticity of different species and populations, as opportunistic diets should increase resilience, while a combination of a specific diet with declines of a major food source is cause for concern.

6.5. Final remarks

Following their 120 million years of existence (since early Cretaceous), marine turtles have survived major past climate changes (Scheyer et al. 2014), including the dramatic changes leading to the Cretaceous-Paleogene mass extinction (~66 Mya), responsible for the disappearance of 75% of life on earth (Schulte et al. 2010). Yet, they now face a much faster rate of change (IPCC 2018, Cheng et al. 2019) along with several human-induced threats that may act synergistically with climate change impacts (Fuentes et al. 2013, Rees et al. 2016). Even if marine turtles survive as a group, species with restricted distribution ranges (i.e. flatback and Kemp's ridley turtles), and individual populations that have been depleted (Hamann et al. 2010), are likely to be most vulnerable. Some populations may be more resilient, however, having spatial and temporal microrefugia that allow for optimal incubation conditions, and may also exhibit foraging plasticity (Abella Perez et al. 2016, Patrício et al. 2019). As the knowledge gaps identified here are addressed, our understanding of what the future will look like for marine turtles will increase. Importantly, future research efforts should be global in scope, rectifying current geographic and species biases (Jeffers & Godley 2016), with more research funded and supported in Africa, Asia, and Central and South America. New techniques, enhanced data sharing, and meta-analytic approaches will all afford excellent possibilities for breaking down the barriers to understanding what the impacts of climate change will be on this charismatic group, and how these impacts may be effectively reduced.

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ARTICLES FOR FACULTY MEMBERS

CLIMATE CHANGE AND SEA TURTLE NESTING

Title/Author	**Estimation of the maternal investment of sea turtles by automatic identification of nesting behavior and number of eggs laid from a tri-axial accelerometer / Jeantet, L., Hadetskyi, V., Vigon, V., Korysko, F., Paranthoen, N., & Chevallier, D.**
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Article

Estimation of the Maternal Investment of Sea Turtles by Automatic Identification of Nesting Behavior and Number of Eggs Laid from a Tri-Axial Accelerometer

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Simple Summary: During the reproduction period, female sea turtles come several times onto the beaches to lay their eggs. Monitoring of the nesting populations is therefore important to estimate the state of a population and its future. However, measuring the clutch size and frequency of sea turtles is tedious work that requires rigorous monitoring of the nesting site throughout the breeding season. In order to support the fieldwork, we propose an automatic method to remotely record the behavior on land of the sea turtles from animal-attached sensors; an accelerometer. The proposed method estimates, with an accuracy of 95%, the behaviors on land of sea turtles and the number of eggs laid. This automatic method should therefore help researchers monitor nesting sea turtle populations and contribute to improving global knowledge on the demographic status of these threatened species.

Abstract: Monitoring reproductive outputs of sea turtles is difficult, as it requires a large number of observers patrolling extended beaches every night throughout the breeding season with the risk of missing nesting individuals. We introduce the first automatic method to remotely record the reproductive outputs of green turtles (*Chelonia mydas*) using accelerometers. First, we trained a fully convolutional neural network, the V-net, to automatically identify the six behaviors shown during nesting. With an accuracy of 0.95, the V-net succeeded in detecting the Egg laying process with a precision of 0.97. Then, we estimated the number of laid eggs from the predicted Egg laying sequence and obtained the outputs with a mean relative error of 7% compared to the observed numbers in the field. Based on deployment of non-invasive and miniature loggers, the proposed method should help researchers monitor nesting sea turtle populations. Furthermore, its use can be coupled with the deployment of accelerometers at sea during the intra-nesting period, from which behaviors can also be estimated. The knowledge of the behavior of sea turtle on land and at sea during the entire reproduction period is essential to improve our knowledge of this threatened species.

Keywords: accelerometer; bio-logging; V-net; *Chelonia mydas*; behavioral classification; ecology; deep learning; conservation; convolutional neural network

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1. Introduction

Estimation of parental investment in sea turtles relies primarily on the measurement of reproductive outcomes of females. Without parental care, female sea turtles favor energy investment in pre-ovipositional allocations and lay several nests of 50 to 130 eggs per breeding season depending on the species [1]. Inter and intra-individual variations in the number of clutches and of eggs laid during a breeding season have been observed within populations suggesting variation in energy invested in the offspring [2–4]. Therefore, measuring clutch size (i.e., number of eggs laid) and clutch frequency (i.e., number of clutches per breeding individual) can be used as indicator of maternal investment in sea turtles. However, both of these parameters are difficult to obtain by long-term population monitoring.

Measuring the clutch size and frequency of sea turtles is tedious work that requires rigorous monitoring of the nesting sites throughout the breeding season. The most common method is based on capture–mark–recapture design: patrols of at least eight hours are carried out every night to survey the nesting sites and identify every female that comes ashore, using a Personal Integrated Transponder(PIT) tag or an unique numbered flipper tag [5–8]. However, this method requires a consequent number of observers performing long continuous trips to cover the entire beach and ensure that no individuals are missed, and thus is an important logistic with expensive costs. Moreover, since it is difficult not to miss any sea turtle, the observed number of clutches deposited by sea turtles is generally lower than the real number [5,9,10]. The number of eggs laid is even more complicated to obtain, as it requires observers to stay with one turtle for almost the entire nesting process counting the deposited eggs [11]. Finally, the capture–mark–recapture monitoring method is impractical for a large population or extensive area. Therefore, there is a crucial need to develop an efficient method to remotely record reproductive outcomes of sea turtles in order to support the intense monitoring effort of field observation.

Few studies have explored the use of new technologies to record reproductive outcomes of nesting sea turtle populations. For example, Blanco et al. [12] used ultrasonography of females' ovaries to visualize their reproductive stage. Ultrasound scans allowed them to identify the remaining number of clutches of every scanned female and thus obtain a more accurate clutch-frequency estimation. However, it was not possible to estimate the number of eggs laid from this method and night patrols were still required [12]. In addition, ultrasonography requires direct and repeated interference with the turtles, which may disturb the animals and affect the nesting process while making it difficult to apply over large geographic areas. Another way to estimate clutch frequency of sea turtles relies on deployment of animal-attached tags throughout the breeding season [8,13,14]. Therefore, Weber et al. [8] tested a combination of Very High Frequency (VHF) radio-telemetry and Argos-linked Fastloc Global Positioning System (GPS) tags. Although VHF transmitters are low cost, they still required direct observations of the females and were ineffective at distance > 1 km. On the other hand, GPS tags allowed remote monitoring and were accurate enough to locate individuals on the beach. However, the location appearing on the beach does not guarantee successful nesting, given the possible abortion of nesting without laying eggs and the large number of U-turns (also known as false crawls) undertaken by sea turtles, especially green turtles (Chevallier, personal observation) [10,15]. In addition, the high cost of Argos-linked Fastloc GPS tags limits their use and the number of equipped females [8].

Accelerometer is a low-cost miniature sensor that can provide high-frequency information about the body movements and postures of animals to which it is attached. It measures static and dynamic acceleration and enables researchers to remotely deduce behaviors for animals that are difficult to observe. Over the past few years, there has been an explosion of its use on both terrestrial and marine species [16], for which direct observations are impracticable. Therefore, a few studies monitored the underwater behavior of sea turtles from accelerometers [17–20], but their interpretation remains difficult without rigorous validation and limits their use on these species [21,22]. Only one study refers to the identification of the nesting behavior of sea turtles from accelerometer [23], while visual validation of acceleration signals is easier to achieve on land than at sea. Such method could be complementary to lighter population monitoring by indicating when and how many times an equipped sea turtle would have come to nest on the beach throughout the breeding period.

The aim of this experimental study is to evaluate the extent to which the accelerometer can remotely measure reproductive output of sea turtles. First, we deployed accelerometers on 14 nesting green turtles and visually monitored their behavior simultaneously. Next, we used this dataset to validate the identification of their nesting behavior from acceleration signals and train a powerful supervised learning algorithm to perform it automatically. For this purpose, we tested a fully convolutional neural network that had already proven effective in automatically identifying the underwater behavior of green turtles [24]. Finally, we tested whether it is possible to estimate the clutch size from the acceleration signal.

2. Materials and Methods

2.1. Data Collection

The field work was carried out in April 2019 at Awala-Yalimapo beach (5.7° N, –53.9° W), French Guiana, South America. We deployed CATS (Customized Animal Tracking Solutions, Oberstdorf, Germany) devices including tri-axial accelerometers on 14 free-ranging adult female green turtles during the nesting process. The acceleration was recorded at a frequency of 20 Hz for the three body axes of the sea turtle (AccX: back-to-front axis, AccY: left-to-right axis and AccZ: bottom-to-top axis). The devices were fixed to the turtle's carapace by four suction-cups allowing us to rapidly operate with minimum disturbance. It took less than a minute to attach the device. In most case, we spotted the turtle going up the beach and waited for its first sand-sweeping to start (see Section 2.2 for further description of sand-sweeping and other nesting behaviors). If the turtle did not seem stressed or was not surrounded by group of humans (adding a source of stress), we quickly set the device during this step on the front of the carapace. Otherwise, we waited until the turtle began digging or even laying their eggs. For the 14 turtles (Table 1), and during the laying process, we checked, using a manual reader (GR250, TROVAN®, Douglas, Isle of Man, British Isles), the presence of a Passive Integrated Transponder (PIT) or injected a new one into the right triceps of the unknown turtles. We measured their Curved Carapace Length (CCL) and Curved Carapace Width (CCW) as described in Bonola et al. [25]. In parallel, the behaviors were visually monitored by an assigned person who recorded the corresponding executed time on a voice recorder. For eight nesting green turtles, for whom a good visualization of the eggs allowed it, an observer counted the exact number of eggs laid per contraction and dictated it to a second person who recorded it with the exact observation time in a voice recorder. The position of a few of the turtles did not allow us to record the number of eggs without disrupting them. So for them, we did not count the laid eggs.

2.2. Labelling of Nesting Behaviors

The nesting behaviors of the sea turtle are similar between the species and the different phases and action patterns were precisely described in several ethograms [26–29]. In this study, we focused on the action patterns that resulted in different acceleration signals and thus identified five behaviors: Sand-sweeping, Digging, Egg laying, Covering, and Walking. Based on the definitions and the characteristics given by Lindborg et al. [28], Sand-sweeping corresponds to the "Body Pitting" and "Camouflaging" phases described in their article since both behaviors encompass the same movements, Digging includes the "Transition period", and Walking represents all the forward movements, as described in the "Ascent" phase in their article. We synchronized the observation time of the behaviors with the acceleration data and visualized them using a rblt package ([30], Figure 1). Throughout the nesting process, green turtles expressed numerous latency periods inter-cutting the behaviors with easily noticeable flat acceleration signals. Therefore, we labelled them from the visualisation of the acceleration signal with an additional behavior: Motionless (Figure 1).

Table 1. Summary of the nesting green turtles' measures and the observed number of laid eggs. CCL= Curved Carapace Length, CCW= Curved Carapace Width. The dashes indicate the individuals for which the number of laid eggs could not be counted.

Individual	CCL	CCW	First Recorded Behavior	Nb of Laid Eggs	Comments
#1	126	122	Egg laying	-	
#2	111	103	Digging	-	
#3	122	109	Sand-sweeping	-	
#4	112	96	Sand-sweeping	-	
#5	115	110	Digging	106	
#6	114	113	Digging	111	
#7	102	94	Digging	93	
#8	112	94	Sand-sweeping	117	
#9	108	98	Digging	103	
#10	128	110	Digging	173	
#11	119	104	Sand-sweeping	93	
#12	105	96	Sand-sweeping	-	Did not lay eggs
#13	117	104	Digging	-	
#14	118	106	Sand-sweeping	97	

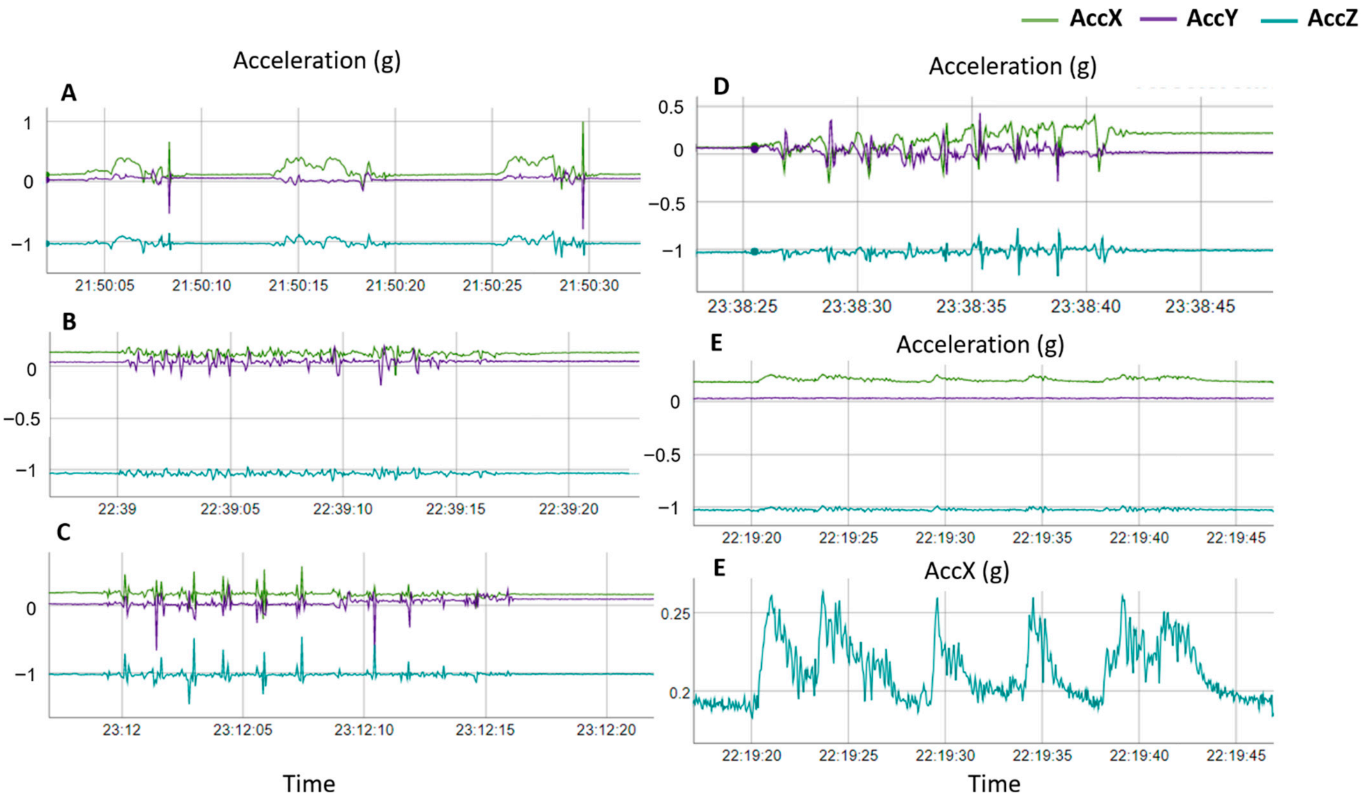

Figure 1. Acceleration signals corresponding to the five behavioral categories of nesting green turtle: Digging (**A**); Covering (**B**); Sand-sweeping (**C**); Walking (**D**); and Egg laying (**E**). We also represent the X-axis of the acceleration of Egg Laying. AccX corresponds to acceleration of the back -to-front body axis, AccY to the left-to-right axis and AccZ to the bottom-to-top axis.

2.3. Automatic Behavioral Identification through Deep Learning

In order to automatically identify the six nesting behaviors from the accelerometer, we trained a fully convolutional neural network: a V-net. The latter was originally developed by Milletari et al. [31] for biomedical 3D image segmentation and an adapted version for the behavioral identification from time series data was tested on underwater free-ranging green turtles and revealed to be efficient [24]. A precise description of the algorithm as well as the processing steps are detailed in Jeantet et al. [24]. Before training the algorithm, we reduced the noise of the acceleration signals on the three axes (AccX, AccY, and AccZ) with a low pass band butterworth filter at 2 Hz and computed the Dynamic Body Acceleration (DBA) from the smoothed signals as described in Jeantet et al. [22]. We randomly split the 14 green turtles into three distinct groups to perform the training/validation/testing datasets. Firstly, when fed with the four previously described descriptors (the smoothed AccX, AccY, AccZ and DBA), the V-net is trained and tuned on eight randomly chosen green turtles and validated on three other individuals. We balanced the behavioral labels in the data batch through a biased random draw of the windows. In particular, we chose a lower probability of randomly drawing Motionless, which is the most frequent behavior. The training and tuning process allowed us to set up the hyper-parameters of the algorithms (depth = 12, window-size = 40, batch = 200 and learning rate = 0.01) and revealed some important confusion between Egg laying and Motionless. Further tests on the effect of each feature suggested that this confusion is mainly induced by AccZ (it adds some non-informative noise). Thus, we removed it and finally trained the neural network with three descriptors: AccX, AccY and DBA. Finally, we tested the model on three green turtles, never seen by the model before, computing the confusion matrix, the global accuracy, the Recall and Precision indicators relative to each of the behaviors as in Jeantet et al. [24].

2.4. Estimation of Laid Eggs

Once the V-net has predicted the six behavioral categories, it became possible to automatically extract the predicted Egg laying stage and to estimate the number of laid eggs. The laying process is associated with a very slight back and forth movement of the sea turtle's body which can be visualized on the X-axis of the accelerometer. Its visualization synchronized with the observed number of laid eggs in the field suggested that a peak on the X-axis acceleration signal corresponded to a contraction (Figure 2). Thus, the number of eggs, related to the number of contractions, was estimated by detecting the number of peaks expressed on the X-axis acceleration signal. Some contractions expressed by the green turtles may be associated with the absence of egg deposition, but they were in the minority and occurred mostly at the end of the egg laying process. Due to their low number, we did not consider these contractions. The hypothesis that the number of eggs laid during one contraction depending on the intensity of that contraction, and thus the associated peak, was also considered, though was not conclusive (Figure 2).

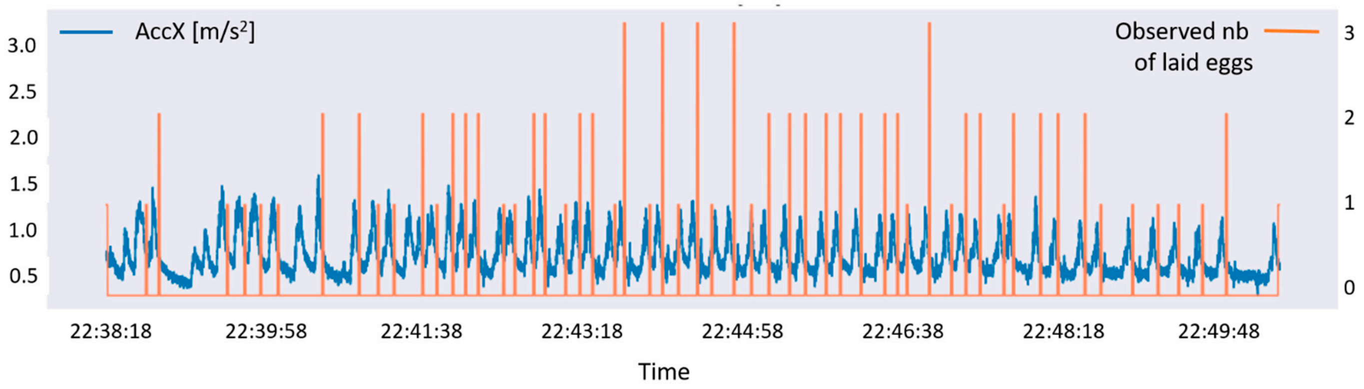

Figure 2. Visualization of the surge acceleration axis (back-to-front or X-axis, in blue) of one green turtle associated with the number of laid eggs counted in the field (in orange).

2.4.1. Cutting off the Egg Laying Period

To automatically extract the accurate Egg laying part from the V-net predictions, we first discarded the false positive identifications, which generally corresponded to very short sequences distributed in the nesting sequence. For this purpose, we performed the next algorithm with each step depicted in Figure 3:

1. Binarize the behaviors sequence: label "1" is assigned to the behavior Egg laying while all the others are labelled as "0" (Figure 3a);
2. Perform a convolution of the binarized sequence with a Gaussian mask whose standard deviation is empirically chosen. The convolved signal is represented in blue as the 'Smoothed density' (Figure 3b);
3. Choose a minimal threshold (threshold = 0.7), and extract the acceleration values associated to the part of the convolved signal which is greater than it (Figure 3b).

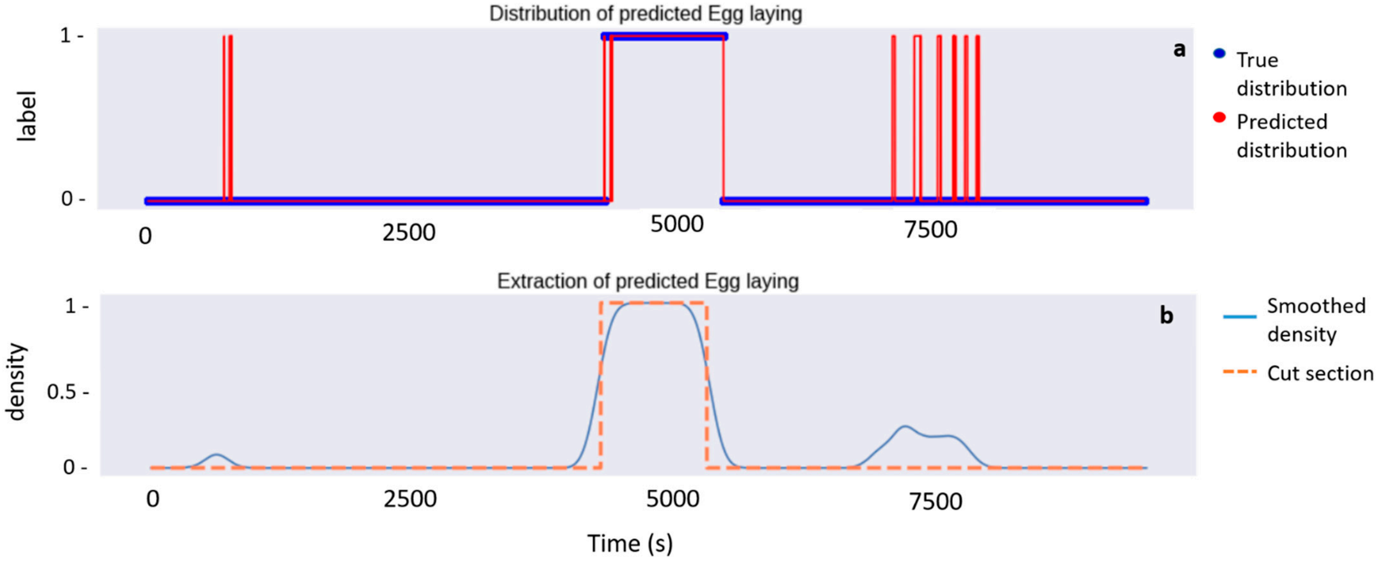

Figure 3. Representation of each step of the extraction of the Egg laying period from the predictions of the V-net for the individual #11. The first panel (**a**) shows the true distribution of Eff Laying over time compared to the predicted distribution by the V-net. The second panel (**b**) shows the smoothed signal of the predicted distribution while the orange dashed line represents the automatically extracted Egg Laying period from which the number of eggs laid is estimated.

2.4.2. Peak Detection

At this point, as it has been concluded that X-axis acceleration contained the largest amount of information for estimating the number of eggs laid, the next analysis was only performed on this axis. In order to augment the precision of peak detection, we firstly smoothed the extracted Egg laying signal using a narrow Gaussian mask. Moreover, we observed a decrease of the average values of the signal all over the laying process, with lower peaks at the end, making their identification difficult compared to the higher peaks at the beginning. We corrected this by subtracting from the trend from its signal, estimated by a second-degree polynomial, adjusted by least-squares approximation. The data are also centered with respect to its average values inside the Egg laying category.

To estimate the number of peaks over the X-axis, assumed to be related to the number of turtle contractions, we ran over the signal a rolling window with a width approximatively equal to the distance between two picks and detected the local maximum for each window. To avoid detecting the same maximum several times, we kept the value only if it was located in the very middle of the rolling window. Finally, a threshold parameter (represented in dotted red in Figure 4) was chosen as a proportion of the median of the signal. Every found local maximum under this threshold was discarded (Figure 4).

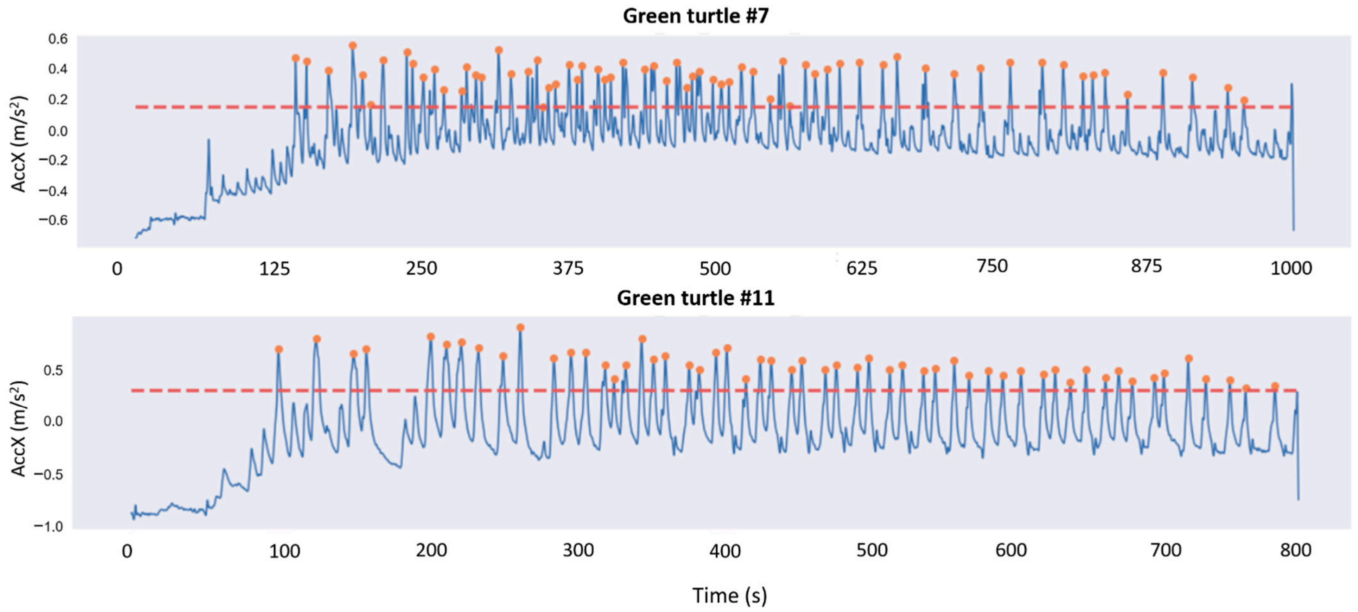

Figure 4. Visualization of the surge acceleration axis (back-to-front or X-axis, in blue) of the laying process of two green turtles with the peaks detected from a rolling window with width of 200.

2.4.3. Estimation of the Number of Eggs

We used the estimated number of contractions to calculate the number of laid eggs. From the egg numbers per contraction recorded in the field (from one to four eggs), we calculated the mean number of eggs laid per contraction per turtle and obtained an average of 1.6 (standard deviation = 0.05). For each turtle, we multiplied the estimated number of contractions by this mean to obtain the estimated number of eggs laid. The mean number of eggs laid per contraction should be reconsidered in a larger population to improve its accuracy.

We tested the entire procedure (from the V-net identification to the estimation of number of laid eggs) on the eight green turtles distributed in the training/validation/testing dataset for which the number of laid eggs has been observed.

3. Results

The V-net predicted the six behaviors (Sand-sweeping, Digging, Egg laying, Covering, Walking and Motionless) with an accuracy of 95%. It correctly identified 97% of the Egg laying dots, corresponding to the highest Recall index (Figure 5, Table 2). The lower Precision index for this behavior (0.79%) was due to Motionless dots being wrongly predicted as Egg laying. However, since the latter occured one time during the nesting process and was very well identified by the V-net, the Egg Laying period clearly differed from the other behaviors when visualizing the activity budget (Figure 6). The misidentifications from the V-net concerned more Covering and Walking that were confused with Sand-sweeping, leading to the lowest Recall and Precision indexes for these two behaviors (Figure 5, Table 2). The visualisation of the activity budget revealed that it was mostly the end of the Covering process that was confused with Sand-sweeping. (Figure 6).

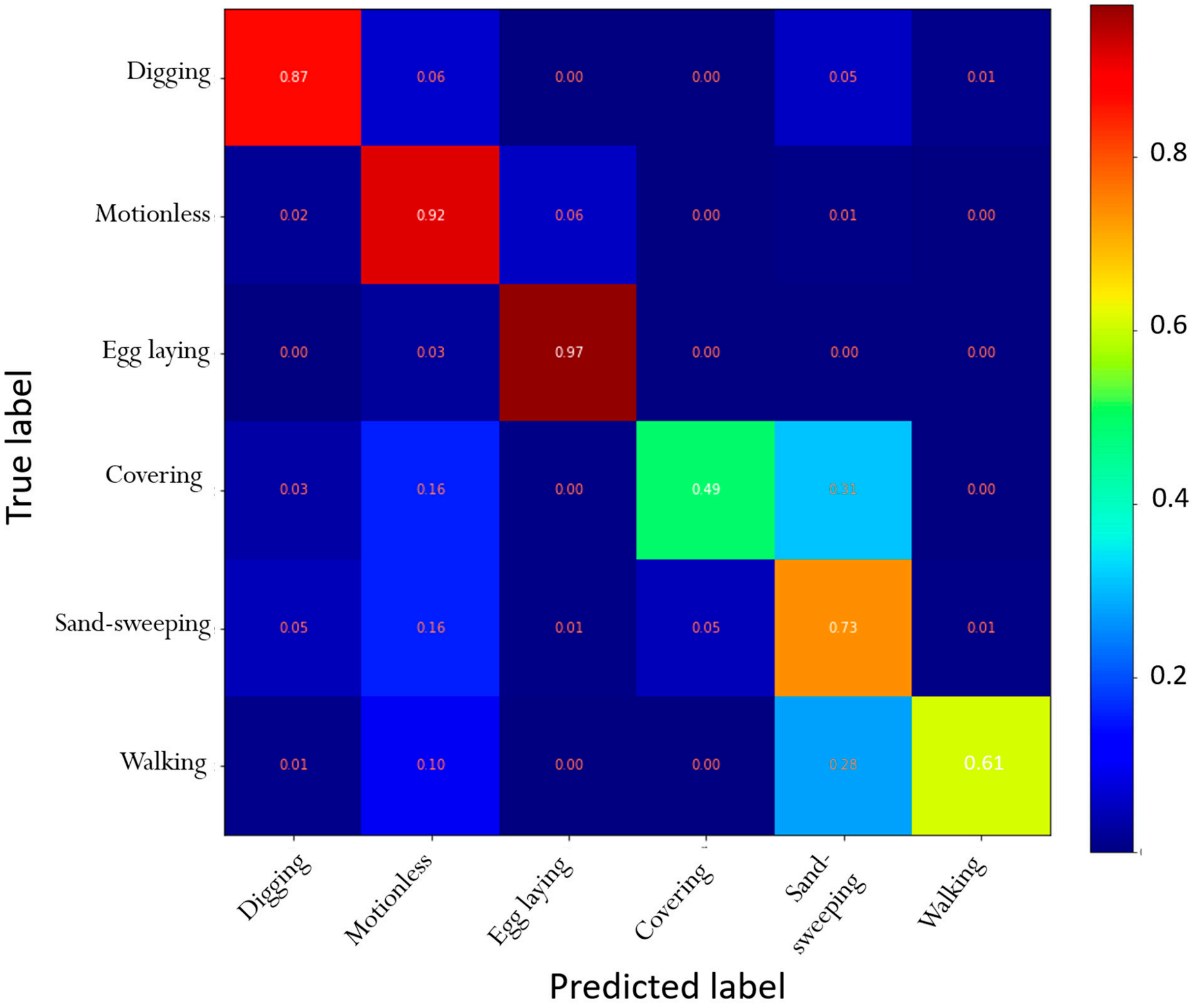

Figure 5. Confusion matrix of the predictions obtained from the V-net for the three green turtles of the validation dataset.

Table 2. Recall and Precision index obtained for the six nesting behaviors from the V-net for the three green turtles of the validation dataset. Accuracy (in bold) measures the ability of the V-net to correctly identify all behaviors as a whole.

	Recall	**Precision**
Digging	0.87	0.79
Motionless	0.92	0.90
Egg laying	0.97	0.79
Filling and packing	0.49	0.72
Sand-sweeping	0.73	0.84
Walking	0.61	0.70
Accuracy		**0.95**

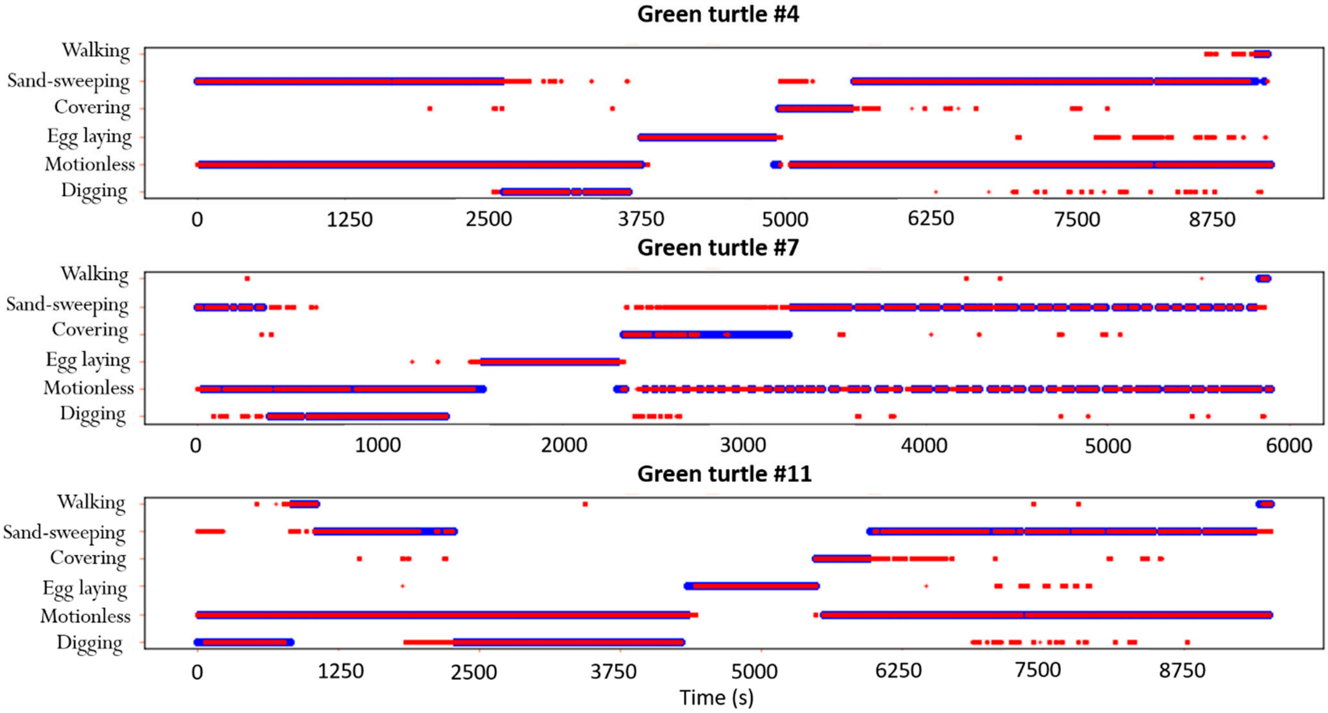

Figure 6. Activity budget of the three green turtles of the validation dataset showing the behaviors inferred by the V-net (in red) compared to actual behaviors (in blue).

The correct identification of Egg laying allowed its automatic extraction with sufficient precision to estimate the number of contractions. Thus, from the V-net predictions, we succeeded in estimating the number of eggs with a mean relative error of 7% (standard deviation = 0.06, Table 3).

Table 3. Estimations of the number of laid eggs for eight green turtles from the Egg laying period identified by the V-net and/or manually extracted from the acceleration visualization compared to the actual observed numbers on the field.

Individual	Nb of Observed Eggs	Nb of Estimated Eggs	Difference	Relative Error
#5	106	101	−5	0.05
#6	111	109	−2	0.02
#7	93	93	0	0.00
#8	117	118	1	0.01
#9	103	117	14	0.14
#10	173	150	−23	0.13
#11	93	88	−5	0.05
#14	97	112	15	0.15
MEAN			−1	0.07

4. Discussion

This study provides the first method to automatically determine the reproductive outputs of the nesting process of green turtles, from animal-attached accelerometers. Using deep learning, we firstly identify the six behaviors expressed by the individuals (Sand-sweeping, Digging, Egg laying, Covering, Walking and Motionless) with an accuracy of 0.95 and a precise detection of the Egg Laying process (Recall index: 0.97). In a second step, we estimate the number of laid eggs from the predicted Egg Laying sequence and find the reproductive outputs with a mean relative error of 7%. The main aim of this method is to support field monitoring of nesting sea turtles by providing a remote method and thus reducing the monitoring effort. In the interests of improving our knowledge of sea turtles, we expect that this method will be a valuable tool for measuring maternal investment in sea turtles and understanding the parameters that influence it.

4.1. Automatic Identification of Nesting Behaviors

The V-net is a powerful algorithm that successfully identifies the six behaviors of the nesting process of the green turtles from the accelerometer with an accuracy of 0.95. Similarly, Nishizawa et al. [23] performed the same task using a Classification and Regression Tree (CART) and obtained an accuracy of 0.86 for the same behavioral categories, but without Motionless. Thus, the V-net represents a major improvement as it does not require pre−processing (no segmentation and hand−crafted feature extraction), while having a better accuracy than the CART. Moreover, this study is the second one to use a V-net to perform behavioral identification from the acceleration signals of green turtles (at sea, [24]). The fact that we used the same architecture, and the same hyper−parameters, on similar but not identical data was a positive time saver, which is also promising for future works using loggers.

The main confusion from the V-net concerns Covering and Sand-sweeping. The visualisation of the activity budget shows that this misclassification appears between the end of Covering and the beginning of Sand-sweeping. This confusion is mainly due that nesting turtles express rear flipper sweeping movements in the two stages [28]. In fact, Covering ends with rear flipper sweeps consecutively to rear knead movements, while the following Sand-sweeping stage begins with simultaneous both rear and front flipper sweeps and is characterised by sweeps of the front flippers alone at the end. Nishizawa and al. [23] also obtained the lowest Recall index associated with Covering. Confusions on behavioral identification from supervised learning algorithms were also revealed on other species for which different behaviors encompass similar mechanistic movements [32–34]. More generally, the automatic behavioral identification from accelerometer are based on the animals' posture and the movements and thus requires the precise definition of the behavioral categories based on these, rather than the function or action of the behaviors. In our case, a more precise identification and annotation of the movements involved in Covering and Sand-sweeping in the field (such as 'rear flipper sweeping', 'front flipper sweeping' and 'covering') would probably improve the precision of the V-net for those two behaviors. However, the main challenge in remote monitoring of sea turtles during the breeding season is to detect the egg laying process because in marine turtles, and more markedly in green turtles, individuals come ashore several times in the same night before laying eggs [10,15]. This is why it is important to detect with certainty if the turtle has laid eggs or not and to understand the reasons for these U−turns. Our study allowed us not only to detect the six behavioral categories of the nesting process, but also a more accurate detection of the Egg laying process by the V-net (Recall index = 0.97).

After this step, the second challenge was to automatically estimate the number of eggs laid, which would thus make it possible to determine the maternal investment during one nesting season.

4.2. Automatic Identification of Number of Eggs Laid

This study is the first to propose a fully automatic method to remotely estimate the number of laid eggs from a bio-logger. The precise detection of the Egg laying process allowed us to automatically extract the associated acceleration signals and estimate the number of eggs laid. We succeeded in estimating the number of eggs laid with a mean relative error of only 7%. However, it remains difficult to identify the main causes of error considering underestimates of the number of eggs laid for some individuals and overestimates for others (Table 3). The parameters that may lead to over- or underestimation are the accuracy of the associated acceleration sequence extraction, the thresholds fixed to identify the number of peaks and the mean number of eggs laid per contraction obtained from field observation (1.6 ± 0.05). The latter is rather constant with an exact value between

1.57 and 1.59 for the three individuals associated with a relative error above 10%. In all cases, these estimation errors remain low with relative errors below 15% for most individuals and highlight the potential of this method for remote monitoring of sea turtles on land during nesting season.

4.3. Perspective of Application

The main aim of the proposed method is, therefore, to support field nesting sea turtles' monitoring while reducing the monitoring effort, via the remote monitoring of nesting sea turtles for estimation of maternal investment. In particular in French Guyana, given that we know the average number of spawns per individual per season for green turtles and the average delay between two successive nesting processes (Chevallier, personal observations), it would become possible to equip several dozen females with bio-loggers at the start of the breeding season and recover them at the estimated end of their nesting season. Therefore, we would go from exhaustive monitoring 7 days a week during 6 months to 30 days of patrols (5 days to equip and 25 days to recover the materials with a large margin of error on the last return of the green turtles to avoid missing them). Although further research is needed to determine the impact of equipment attached to turtles, the miniaturization of the accelerometer allows for miniature loggers (weight less than 5 g and size 22 × 13 × 8 mm, http://www.technosmart.eu, accessed on 15 February 2022) making this long tracking feasible. Therefore, this long term monitoring of sea turtles from bio-loggers during the whole breeding period would allow researchers to know precisely the clutch frequency, its clutch size and variation during the breeding season for a representative part of a population, and therefore the estimation of their maternal investment, while reducing the patrol time.

Furthermore, the estimation of the reproductive effort of nesting females on land is complementary to the use of the accelerometer on green turtles at sea. Indeed, the proposed method is part of a more general framework where a validation and automatic identification of the underwater behaviors of green turtle from accelerometer data have already been achieved [22,24]. It would then be possible, using accelerometers deployed over the entire breeding season, to describe the underwater behaviors expressed by green turtles, during two successive nesting processes, i.e., the intra−nesting period, and to estimate the number of laid eggs on land. All this information is essential to study the cause−effect relationships between the energy strategy undertaken at sea and the maternal investment. Indeed, inter- and intra-population variations in reproductive outputs have been observed suggesting the influence of the environmental resource availability and the fitness of the individuals [2,4,35]. Whereas the clutch frequency and size are indicative of the success or failure of the individual's energetic strategy in response to the environmental conditions, the identification of the underwater behaviors enable the identification of this strategy during the inter-nesting period. Combined with environmental data (food availability, water temperature, and ocean current), it could help researchers to identify the extent to which environmental factors influence this energetic strategy and thus the maternal investment. The parallel monitoring at sea and on land could be a key parameter for understanding the adaptive capacities of marine turtles in the context of climate change.

5. Conclusions

This experimental study initiates the first steps towards an efficient method of the sea turtles' reproductive outputs recording from low-cost miniature sensors. Such an approach allows noticeable reduction of monitoring effort and minimizing of human error.

Recovery of bio-loggers, few weeks later, can still be tedious work, but the development of satellite-relay data tags with on-board processing represents a promising alternative. Indeed, it is already possible to remotely transmit a summary of the tri-axial acceleration from satellite-relay data tags [36–38] and to implement the learning algorithm into the logger [39]. This next step would enable the researchers to remotely, and almost in real time, follow the nesting behaviors of the equipped individuals (with the estimation of the number of eggs laid) and to relate this information with their behaviors at sea over long periods (pre−nuptial migration, breeding season, post−nuptial migration).

All of these associated technologies will allow the acquisition of acquire knowledge that has never been obtained until now, of the influence of marine environmental parameters on individual's behavior at sea over long periods (migrations) and the consequences on their maternal investment during reproduction periods. This challenge seems very accessible in the near future.

Author Contributions: D.C. contributed conception and design of the study; D.C., L.J., F.K. and N.P. contributed to data acquisition; V.V. built the V-net architecture and adapted it to the 1D data; L.J. and V.H. performed the data acceleration analysis and applied the V-net on the sea turtle dataset; L.J., V.H. and V.V. wrote the first draft of the manuscript; and D.C., F.K. and N.P. contributed critically to subsequent versions. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: This research was conducted under permits R03-2017-05-15-003 to DC. This study meets the French legal requirements where it was carried out, and follows all institutional guidelines. The protocol was approved by the Conseil National de la Protection de la Nature and the French Ministry for Ecology, Sustainable Development and Energy, which act as an ethics committee in French Guiana. The fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of French Guiana (Cayenne, France), in order to minimize the disturbance of animals.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

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CLIMATE CHANGE AND SEA TURTLE NESTING

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Impact of marine heatwaves for sea turtle nest temperatures

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There are major concerns about the ecological impact of extreme weather events. In the oceans, marine heatwaves (MHWs) are an increasing threat causing, for example, recent devastation to coral reefs around the world. We show that these impacts extend to adjacent terrestrial systems and could negatively affect the breeding of endangered species. We demonstrate that during an MHW that resulted in major coral bleaching and mortality in a large, remote marine protected area, anomalously warm temperatures also occurred on sea turtle nesting beaches. Granger causality testing showed that variations in sea surface temperature strongly influenced sand temperatures on beaches. We estimate that the warm conditions on both coral reefs and sandy beaches during the MHW were unprecedented in the last 70 years. Model predictions suggest that the most extreme female-biased hatchling sex ratio and the lowest hatchling survival in nests in the last 70 years both occurred during the heatwave. Our work shows that predicted increases in the frequency and intensity of MHWs will likely have growing impacts on sea turtle nesting beaches as well as other terrestrial coastal environments.

1. Introduction

Extreme weather events have massive ecological impacts across terrestrial, aquatic and marine habitats and can fundamentally shape ecosystems [1]. In the oceans, there is intense interest surrounding the ecological and socio-economic impacts of long-term ocean warming including discrete periods of prolonged anomalously warm water at particular locations, known as marine heatwaves (MHWs) [2,3]. MHWs can have a wide-range of impacts including major coral bleaching and mortality, seagrass and kelp die-offs, disease outbreaks and fisheries disruptions [4–7]. Impacts have been reported across the globe [8] and importantly even remote, relatively pristine areas that are far from localized anthropogenic impacts are not immune to the impacts of MHWs [9]. While the impacts of MHWs have been well documented for a range of coastal species and ecosystems, it is less well known if MHW impacts extend to adjacent terrestrial systems. For example, sea turtles nest on sandy beaches, i.e. close to the sea, and it is unknown whether their incubation conditions are impacted by MHWs. Indeed, there has been a call for a better understanding of how climate change will impact the biota of sandy beaches [10]. This question of MHW impacts on beaches is of conservation importance since incubation temperatures for sea turtles impact both the sex ratio of hatchlings as well as embryonic survival [11], giving rise to major concerns that generally

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warming conditions might cause the production of single-sex cohorts and so ultimately cause population extinctions [12].

In the austral summer of 2015/2016, a major coral-bleaching event associated with an MHW occurred in the Chagos Archipelago, a remote island group in the equatorial Indian Ocean that was previously known to host some of the most pristine coral reefs in the world [9]. Here, we take advantage of the recording of beach and water temperatures before, during and after this coral-bleaching event to consider the implications of the MHW for sea turtle incubation conditions and hence hatchling survival and sex ratios. We then use long-term temperature records to place this MHW in a multi-decadal context and consider the likely impacts of the increasing occurrence of MHWs for sea turtle nests, as well as other wildlife close to the sea.

2. Material and methods

Temperature loggers (Tinytag Plus 2 model TGP-4017, Gemini Data Loggers, UK, accurate to less than 0.5°C) were buried at nest depths (30, 50, 70 and 80 cm) to record the sand temperature every 4 h on a key nesting beach for hawksbill and green turtles on the southern coast of the island of Diego Garcia (7.42° S, 72.45° E) within the Chagos Archipelago (Indian Ocean). Diego Garcia hosts the highest nesting density of hawksbills and green turtles in the region. It is also an important nesting location for both turtle species in the context of overall nesting numbers across the western Indian Ocean [13]. Loggers were deployed to capture the extent of thermal variation across nesting zones on the beach, see [14] for details, and covered nesting depths for both hawksbill and green turtles. Loggers were placed at nest depths, but not inside nests. Across the range of depths, depth-related differences in sand temperature at this site are minimal, averaging 0.1 °C [14]. In total, we analysed data from 52 sand temperature loggers deployed between October 2012 and August 2019. Loggers recorded data for an average 19.9 months (s.d. = 6.6 months, min = 2.4 months, max = 35.6 months). Typically, there were between four and 10 loggers used in each mean monthly sand temperature calculation (median = 8). At this site, hawksbill turtles show a distinct nesting peak during October–February, and green turtles nest year-round with elevated activity during June–October [13].

Air temperature data for a 10 × 10 degree area around the Chagos Archipelago (2–12 °S and 66–76 °E) were obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) through the National Center for Atmospheric Research (NCAR) (https://rda.ucar.edu/datasets/ds548.0/). The Enhanced ICOADS Monthly Summary Release 2.5 at 2-degree spatial resolution was used. Visual inspection showed that air temperatures were broadly homogeneous and so the exact area used in this analysis did not impact our overall conclusions. In addition, we extracted Hadley sea surface temperature (SST) data for the same geographic area from the UK Meteorological Office (http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html). We used these freely available datasets, rather than local measurements, as they provide global coverage and have data extending back many decades. Hence these datasets can be used to reconstruct past conditions and our approach detailed here can be easily applied to nesting sites around the world.

Water temperatures on the coral reef at Diego Garcia were measured with Hobo U22 data loggers recording at 2 h intervals and accurate to less than 0.2°C. Loggers were secured at 15 m on the reef and protected against fish bites by short lengths of pipe. Rainfall data collected at Diego Garcia Airport were obtained from the airport meteorological station.

We calculated monthly means from our measurements of sand temperatures on beaches and reef water temperatures. This served to make these local measurements directly comparable with the ICOADS and Hadley datasets which are both supplied as monthly means. We investigated the relationship between our empirical sand temperatures and historical environmental variables using a stepwise multiple regression in which ICOADS air temperatures, ICOADS SST, Hadley SST, local reef water temperatures and precipitation were entered as predictor variables. Degrees of freedom in this analysis were adjusted for serial autocorrelation using the modified Chelton method [15]. We further explored the potential causal pathways present in our time series using a Granger causality test [16]. This approach represents a measure of forecasting over and above that provided simply by temporal correlations and helps point towards causal links.

For our predictive models of primary hatchling sex ratios and in-nest hatchling survival, (i.e. hatchling success), we assumed that metabolic heating within clutches averaged 1.1°C by the middle third of development (i.e. the period when sex is determined during incubation), as reported for hawksbill and green turtles in a recent review [17]. This value for metabolic heating was added to the mean monthly sand temperatures recorded at nest depths. We used the general relationships between incubation temperature and hatchling sex ratios and hatchling success [11], which assumed a pivotal temperature (i.e. the temperature at which the primary sex ratio is 50 : 50) of 29.1°C. In these relationships, greater than 99% males are produced at temperatures less than 26°C, greater than 99% females above 32°C and hatchling success declines to zero above 36°C. The same relationships were assumed for both species.

3. Results

We obtained the mean sand temperature at nest depths for 61 separate months between October 2012 and August 2019. Across these 61 months, temperatures recorded (i) at nest depths on the nesting beach, (ii) at 15 m on local coral reefs and (iii) at the sea surface more broadly across the Indian Ocean (ICOADS SST and Hadley SST) all showed similar patterns and were all tightly correlated (figure 1), i.e. warm air and sea conditions in the ocean across that broad region were also reflected in warm water conditions on the local reef and in the sand on nesting beaches. Therefore, historic air and sea temperatures across this broad region can be used to reconstruct past sand temperatures. In all these temperature time series, the maximum temperatures were recorded in early 2016.

A stepwise multiple regression showed that Hadley SST alone was the best predictor for sand temperature: mean monthly sand temperature = 1.066 × Hadley SST − 2.375 ($F_{1,13.3} = 193.1$, $p < 0.001$, $r^2 = 0.76$). Put simply, a 1°C rise in SST translated into a 1.07°C rise in sand temperature (95% confidence interval = 0.91–1.22), so an MHW would translate into warmer turtle nest conditions. In addition, we found significant Granger causality ($p < 0.05$) in the relationship between mean monthly Hadley SST and mean monthly sand temperatures, i.e. when past values of SST were used in a regression model to predict future values of sand temperature (with a lag of 1 month) after adjusting for past values of sand temperature. This result further reinforces the view that variations in SST strongly influenced sand temperatures.

Modelled hatchling sex ratios and hatchling success predicted from the mean monthly sand temperature both showed impacts of the hottest temperatures in early 2016 (figure 2*a,b*). The modelled hatchling sex ratio varied seasonally from around 10–20% female in the coolest months (July

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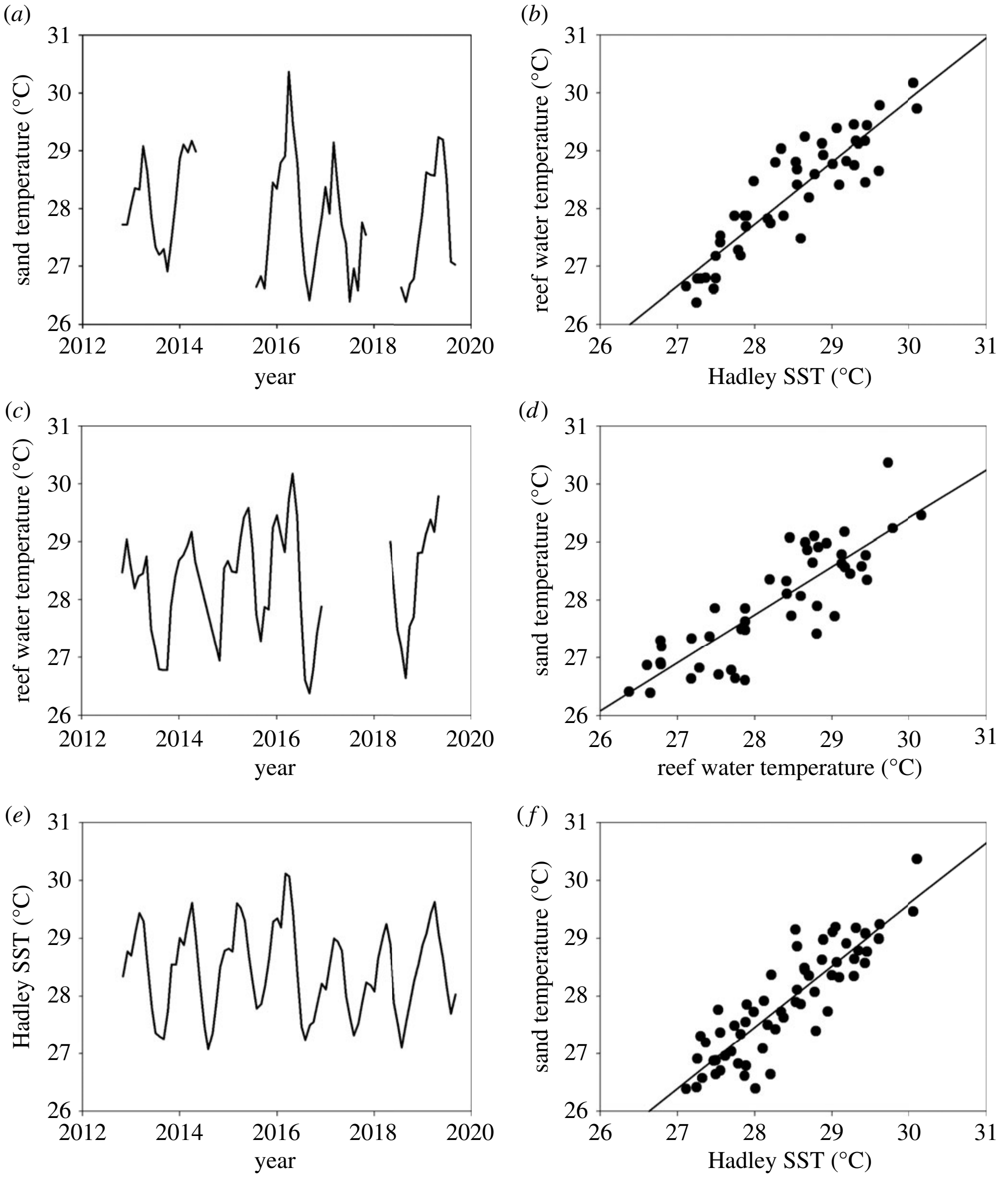

Figure 1. Time series of mean monthly (*a*) sand temperature at nest depths on Diego Garcia, (*b*) coral reef water temperature at 15 m on Diego Garcia and (*c*) Hadley SST measured more broadly across the Indian Ocean. The warmest months in all time series occurred in early 2016, corresponding with an MHW and major coral-bleaching event. The relationships between mean monthly (*d*) water temperature at 15 m on Diego Garcia and Hadley SST, (*e*) sand temperature at nest depths on Diego Garcia and water temperature at 15 m on Diego Garcia and (*f*) sand temperature at nest depths on Diego Garcia and Hadley SST. In each case, these regression equations were highly significant ($p < 0.01$) with r^2 values of 0.81, 0.72 and 0.77, respectively. Due to logistical constraints of working at this remote nesting area, there was not a continuous rolling deployment of loggers, so some gaps when no loggers were deployed remain in our time series.

and August) to around 80–90% female in the warmest months (February–March). The most extreme modelled female-biased hatchling sex ratio (95.6%) was predicted for March 2016. The modelled hatchling success was generally around 85–90%, but the lowest value (71%) was predicted for March 2016. The long-term (1950–2019) Hadley SST data show a 70-year trend of generally rising water temperatures in the region superimposed on the annual cycle, with the mean annual rise in temperature being 0.015°C (i.e. 0.15°C per decade) (figure 2*c*). March 2016 was the warmest month in this 70-year time series. There was a tendency for more extreme warmer temperatures as the time series progressed.

4. Discussion

We showed that an MHW that caused a major coral-bleaching event [9] also affected sand temperatures at sea turtle nest depths, with likely consequences for hatchling survival and sex ratios. This finding is noteworthy given the trend for increasing frequency and intensity of MHWs globally [8,18] and suggests that wider consideration should be given globally to MHW impacts on sea turtle incubation conditions. More broadly, our results suggest that MHW impacts are not confined to marine habitats, which have been the focus of previous studies [7].

The ecological impacts of the MHW for corals and sea turtle hatchlings were very different. During the 2016 coral-bleaching event in the Chagos Archipelago, coral cover on reefs dropped from around 40–50% to 10% on average and the reefs have been slow to recover [9]. Measured growth rates for several coral species in 2018–2019, following this bleaching event, were also comparatively low, suggesting prolonged effects of heat stress on coral physiology [9]. Concerns for the future of coral reefs in the region are heightened by the predicted increases in the frequency of severe bleaching events in the coming decades [19]. Set against the

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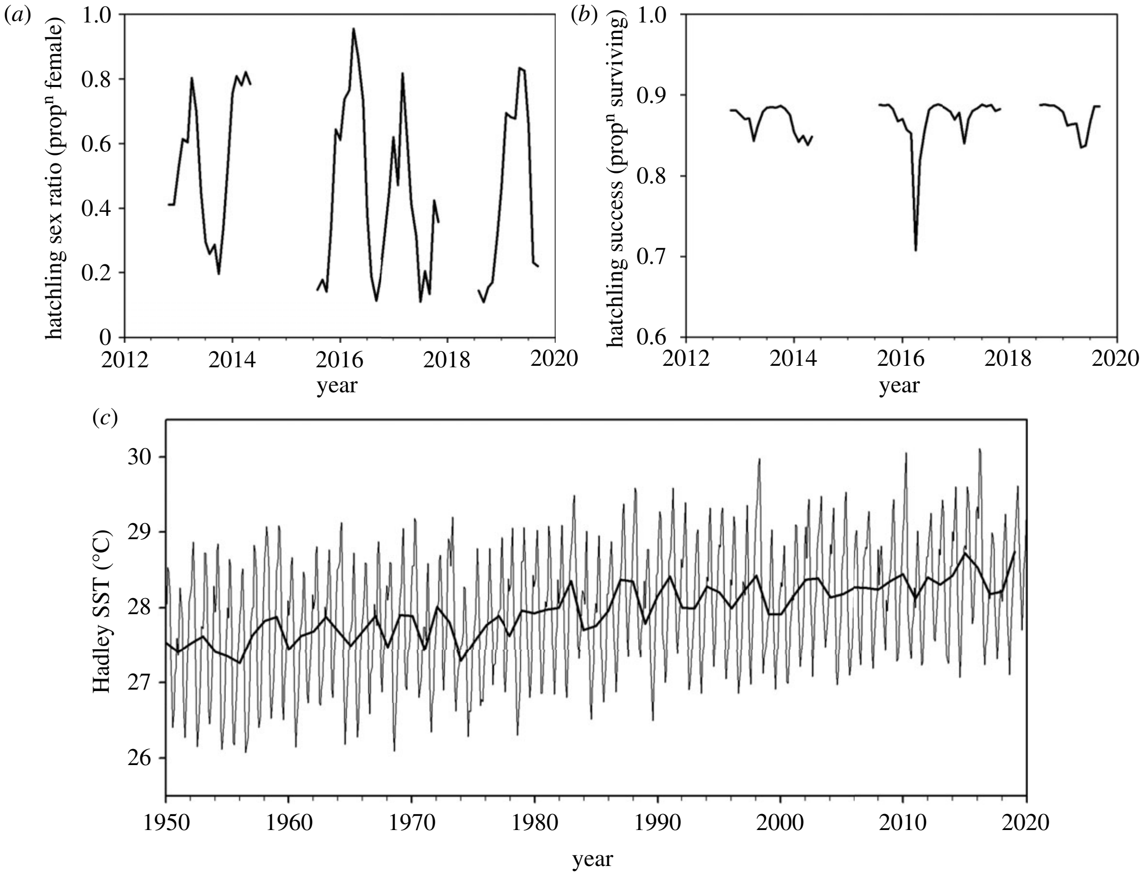

Figure 2. Based on the mean monthly sand temperature (figure 1*a*), the predicted (*a*) hatchling sex ratio and (*b*) hatchling success on Diego Garcia. In both cases, extreme values were predicted for March 2016, which was the warmest month in the time series. (*c*) The time series of mean monthly Hadley SST around the Chagos Archipelago. The fitted line is the mean annual temperature which increased linearly over time at a mean rate of 0.15°C per decade ($F_{1,68} = 162$, $p < 0.001$).

dire implications of MHWs for coral reefs in the region, our results suggest that for sea turtles the implications are likely to be far less severe, e.g. short-term changes in hatchling sex ratios and decreases in hatchling success.

The different impacts of the 2016 MHW on corals and turtle nests do not reflect differences between the respective temperature rises for coral reef and sandy beach environments. Rather the different responses reflect how close corals versus sea turtle nests were to their thermal tolerances. The reef water temperatures in the Chagos Archipelago are seasonally 28–29°C, which is very close to the thermal limits for corals and hence a slight increase in temperature can have very marked impacts [9]. By contrast, the general sand temperatures at nest depths on Diego Garcia are relatively low [14] and well within the thermal tolerances for developing embryos [20]. Nevertheless, our conclusion that MHWs can impact sea turtle nest temperatures has important broader implications. While sand temperatures at nest depths on Diego Garcia are relatively cool, in other locations much warmer sand temperatures often predominate and are of concern [12]. For example, across the globe, highly female-skewed sea turtle hatchling sex ratios dominate because incubation temperatures are generally well above the nominal pivotal temperature of 29°C [21]. In cases where incubation temperatures are already very high, the additional impact of MHWs is likely to be catastrophic, driving high hatchling mortality and reducing male production. Furthermore, if the trend for rising SSTs around the Chagos Archipelago and elsewhere continues as predicted [7], then the impact of future MHWs for hatchling sex ratios and hatchling mortality will grow. In short, we suggest that MHWs need to be considered an important and growing threat for sea turtles [22].

Given the concerns that we highlight of MHWs and rising temperatures for sea turtle incubation conditions, potential ways in which nest temperature rises might be mitigated need consideration, such as phenological shifts in nesting seasons [23] and artificially cooling nests [24]. Furthermore, our model could be improved if local measurements of metabolic heating were available. Direct measurements of hatchling sex ratios will also help refine estimates for the impact of MHWs.

The Hadley SST data suggest that the water temperatures associated with the 2016 coral-bleaching event were exceptional in the last 70 years, but also form part of a trend of warming conditions, which reiterates concerns for the future of coral reefs in the region [9,25]. It is also noteworthy that a previous coral-bleaching event was recorded in the Chagos Archipelago during the austral summer of 1997/1998 [9], as well as more broadly across the Western Indian Ocean [7], and the Hadley SST data again showed very warm conditions in March and April of that summer. Our findings also suggest, therefore, that around the world historical conditions in focal coastal areas might be reliably reconstructed using freely available broad-scale environmental measurements, albeit it is important, as done here, to first establish that broad-scale measurements reflect local conditions. In this way, observations in coastal areas might be placed into a much longer context of change occurring over many decades.

Ethics. The study was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory

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Administration (BIOTA) of the UK Foreign, Commonwealth and Development Office. The study was endorsed through research permits (0002SE12, 0002SE14, 0007SE15, 0002SE17, 0006SE18, 0009SE18, 0004SE19, 0006SE19, 0011SE19) from the Commissioner's Representative for BIOT and research complied with all relevant local and national legislation.

Data accessibility. The data are provided in the electronic supplementary material [26].

Authors' contributions. G.C.H. conceived the project. J.O.L., W.J.C. and G.C.H. led the data analysis. N.E., G.C.H. and J.O.L. deployed the sand temperature loggers. C.S. deployed the water temperature loggers. G.C.H. led the writing with J.O.L. All authors contributed to drafts and approved the manuscript. All authors agree to be held accountable for the content.

Competing interests. We declare we have no competing interests.

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CLIMATE CHANGE AND SEA TURTLE NESTING

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Influence of climate and tides on the nesting behaviour of sea turtles

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ABSTRACT

A combination of climatic and environmental factors influences, and potentially guides, certain life-history processes, such as breeding. Sea turtle females may wait offshore for the optimal conditions to nest, but these environmental cues remain mostly unknown. Our aim was to identify climatic and tidal influences on nesting for leatherback turtles (*Dermochelys coriacea*) and try to find any specific conditions that induced them to abort the nesting attempt. To assess these issues, the beach in *Pacuare Nature Reserve*, on the Caribbean Costa Rica, was monitored from 2010 to 2015. Models showed that high atmospheric pressure and wind speed favoured nesting but high rainfall discouraged successful nesting; high and low tides were negatively correlated with nesting, suggesting that turtles avoid nesting when tidal cycles reach their extremes. Overall, climatic features likely related to storm episodes, and extreme tidal ranges, appear to influence leatherbacks' nesting behaviour. Therefore, the steady increase in intense storm occurrence predicted by climatic projections might represent an additional obstacle to the survival of this species.

1. Introduction

Despite the encouraging evidence on global sea turtle populations indicating that abundance is increasing rather than decreasing across the globe (Mazaris et al., 2017), improving our knowledge on the biology and behaviours of the species is critical. This need is even more pronounced under the risk of climate change, which could represent a major issue regarding the conservation of marine ecosystems (MacLean and Wilson, 2011). It can be difficult to predict its effects even though some trends have already indicated that human activities are leading to rapid changes in ocean surface temperatures by increasing global average temperatures through a raise in atmospheric greenhouse gas concentration (Hoegh-Guldberg and Bruno, 2010). Ecosystems can suffer both direct and indirect impacts through many of climate change's effects. Besides, anthropogenic pressure might intensify the vulnerability of natural systems (Hopkins et al., 2016). Sea turtles have developed adaptive mechanisms but there is a need to test if they will adapt to new climate scenarios. For instance, effects of sea level rise have already begun affecting sea turtle populations (Almpanidou et al., 2016; Katselidis et al., 2014; Fuentes et al., 2011), and altering nesting behaviours (Rivas et al., 2016a). Fish et al. (2005) reported that up to 30% of beach areas could be lost due to sea level rise which would force sea turtles to migrate, and therefore, to seek for less vulnerable nesting beaches.

Some studies suggest a likely increase in rainfall by 0.2 to 0.3% per decade over tropical areas (10°N to 10°S) and a decrease by 0.3% in sub-tropical zones (10° to 30°N) with a 70% of certainty (Houghton et al., 2007). The inter-annual variation in tropical and sub-tropical regions is rather large (Santidrián-Tomillo et al., 2015); however, there is evidence that both the intensity and duration of stormy events have increased since the 1990s (Goldenberg et al., 2001; Patino-Martinez et al., 2014). If this trend continues, sea turtle resilience could be affected, considering that protracted rainfalls decrease reproductive output of sea turtles (Rivas et al., 2018).

The Caribbean atmospheric circulation is affected by climatic phenomena such as the El Niño Southern Oscillation (ENSO), which seems to have become more frequent in the past few decades (Giannini et al., 2001a), causing extreme dry and wet periods in the Caribbean, thus carrying altered wind regimes and temperatures (Giannini et al., 2001b; Hetzinger et al., 2010).

Sea turtles are distributed along the tropical and sub-tropical regions around the globe, even reaching boreal waters – in the case of leatherbacks. Their foraging and breeding areas are spatially separated, and adult individuals repeatedly migrate between them during their lifecycle (Plotkin, 2003). Environmental factors are known to influence reproductive migrations. For instance, Schofield et al. (2010) found that

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turtle movements in and out of their breeding sites are affected by differences in the barometric pressure. The start of the nesting season and the length of the inter-nesting intervals seem to be driven by sea temperature (Hays et al., 2002; Schofield et al., 2009). However, the environmental cues that nesting females might follow when emerging from the sea keep being mostly unknown (Pike, 2008). Mass nesting events are also triggered by specific climatic conditions. At Pacific Costa Rica, ridley turtles (*Lepidochelys olivacea*) can wait up to 63 days, until the end of the rain season, before emerging from the sea in arribada (Plotkin et al., 1997). In India, olive ridley nesting females seek for low saline waters, low south-easterly waves and local wind bursts, and nest within an interval of one or two days around the new and full moons (Barik et al., 2014). At Ascension Island, a study determined that the maximum air temperature was the main cue that green turtles *(Chelonia mydas)* followed to nest (Godley et al., 2001). In Zakynthos, Greece, drops in barometric pressure influenced inter-nesting foraging rests for loggerhead turtles (*Caretta caretta)* (Schofield et al., 2010). In Florida, USA, researchers have found a relation between tidal cycles, ocean temperatures and turtle nesting (Pike, 2008). To date, multiple variable models seldom been explored, even though they may help understanding the nightly variation in the number of nesting turtles. For instance, Pike (2008) found that the nesting of loggerhead turtles (*Caretta caretta*), in Florida, was positively correlated with the number of rainy nights and moderate tidal cycles – out of 15 environmental variables, both atmospheric and oceanic.

Despite the ongoing research effort, nesting-driving environmental cues still remain unclear for most sea turtle species. In the case of leatherback turtles (*Dermochelys coriacea*), no studies have been made in order to detect what are the climatic features that increase the probability of their nesting. Leatherback from the North-Western Atlantic are categorized as Endangered by the IUCN Red List The IUCN red list of threatened species, 2019: e.T46967827A83327767, 2019, although most populations are Critically Endangered (Tiwari et al., 2013). This species nests in tropical and subtropical beaches (Patino-Martinez et al., 2014) with a 2–3 year remigration interval for the Western Atlantic population (Rivas et al., 2016a), laying up to 11 nests in a season (Kamel and Mrosovsky, 2004). Their foraging grounds, on the other hand, are located in colder waters (Neeman et al., 2015). Thus, climate conditions are very likely to influence their nesting activity (Saba et al., 2007). Atlantic holds the largest leatherback population globally (Rivalan et al., 2006) and *Pacuare Nature Reserve*, on the Caribbean coast of Costa Rica, hosts an average of 142 nests per km (Rivas et al., 2016b), an excellent site for research on leatherback turtles behaviour.

Researching on the factors that influence leatherbacks' nesting activity will ultimately help us to understanding more in detail how climate change and anthropogenical threats may affect this marine species. Consequently, the main aim of this study is to find if leatherback turtles are following any environmental cues to emerge and nest, including maximum and minimum temperatures, rainfall, wind speed and direction, barometric pressure, sea surface temperature as well as high and low tides.

2. Materials and methods

2.1. Study site

We collected nesting data in *Pacuare Nature Reserve*, located on the Caribbean coast of Costa Rica (Fig. 1). The beach is delimited by the Pacuare river mouth to the North (10°13′17″N, 83°16′39″W) and the Mondonguillo lagoon to the South (10°10′00″ N, 83°14′00″ W), and is approximately 5.7 km long. This beach hosts high leatherback nesting density (Rivas et al., 2016b). High-energy swell and medium steep slopes typify this sandy shoreline, and no major anthropogenic disturbances are found close to the beach. This region features semidiurnal tidal cycles, with two high and two low tidal cycles every 24 h period.

2.2. Nesting activity

We conducted night patrols during the entire nesting season, beginning on March 1st and ending on September 31st. These patrols lasted from 8 pm to 4 am. In addition, we also conducted morning counts at 5 am to record all the nests and aborted nesting attempts occurred during night-time. To develop this study, we required the total number of nightly activities, making a distinction between successful nesting attempts and aborted nesting attempts. We considered a nesting attempt successful (‘nest’ from now on) when we found a body pit, an area where sand had been disrupted, and sand spray was present. A nesting attempt was considered as aborted when a body pit was not found adjoining the turtle tracks, or a body pit did not contain any remains of sand spray (Rivas et al., 2016a). We included six consecutive nesting seasons in the study, from 2010 to 2015, during which data had been collected following a standardized methodology that ensures minimized disturbance on the nesting beach (Rivas et al., 2016b).

2.3. Environmental variables and statistical analyses

In order to assess whether the environmental conditions have an effect over the proportion of nests and aborted attempts happening nightly, we calculated the degree of correlation between the two variables (Pearson's correlation coefficient). If they are poorly correlated, the variation in nesting success between nights would be due to other factors, and the next step would involve identifying what environmental conditions influence the nesting activity.

The environmental variables considered in the analyses included sea surface temperature, barometric pressure, maximum and minimum air temperatures, daily rainfall, tidal data, daily predominant wind direction with 8 different categories, and daily average wind speed. We used sea surface temperature (SST) data modelled for a point located 13 km South of the nesting beach (10.1°N 83.1°W) (Fig. 1). The data were retrieved from the National Centre for Ocean Forecasting (NCOF) through the OSTIA system (Operational Sea Surface Temperature and Sea Ice Analysis), which uses satellite data provided by the GHRSST project together with in-situ observations, and performs an analysis using a variant of optimal interpolation (OI) described by Martin et al. (2007), obtaining values in a 1/20° resolution.

The Centre of Investigation about Marine Science and Limnology (CIMAR) provided tidal data, and we included both maximum and minimum daily values in the analyses. The National Meteorological Institute of Costa Rica (IMN) provided datasets for mean daily barometric pressure, maximum and minimum air temperatures, daily rainfall, wind speed and wind direction. Both tidal and atmospheric variables were recorded at the closest meteorological station, at Limón airport, located 30 km South of the beach, on a coastline with very little variation (Fig. 1). To test which combination of variables offered a better prediction of the nesting activity, we ran a GLMM (Generalized Linear Mixed Model). We selected a binomial distribution with a logit link function, and the response variable of the model combined the number of nests (1) and aborted attempts (0) logged on each day as a ratio. We standardized all the continuous environmental variables to account for differences in magnitude and included them as fixed predictors in our model. Wind direction was a categorical variable with 8 levels, and we included it as a random term in order to reduce the number of parameters in the model. Models including it as a fixed term failed to converge. We accounted for the seasonal variation in nesting activity (Fig. 2) by including the Julian date nested within year as random intercepts. We fitted a global model that included all the predictor variables, ran all possible combinations and ranked them according to AIC values, starting from the model with the lowest value. We selected the most parsimonious model with a $\Delta AIC < 2$. We used package lme4 (Bates et al., 2015) from R (R Core Team, 2016) in the analysis and we considered statistical significance at $\alpha < 0.05$.

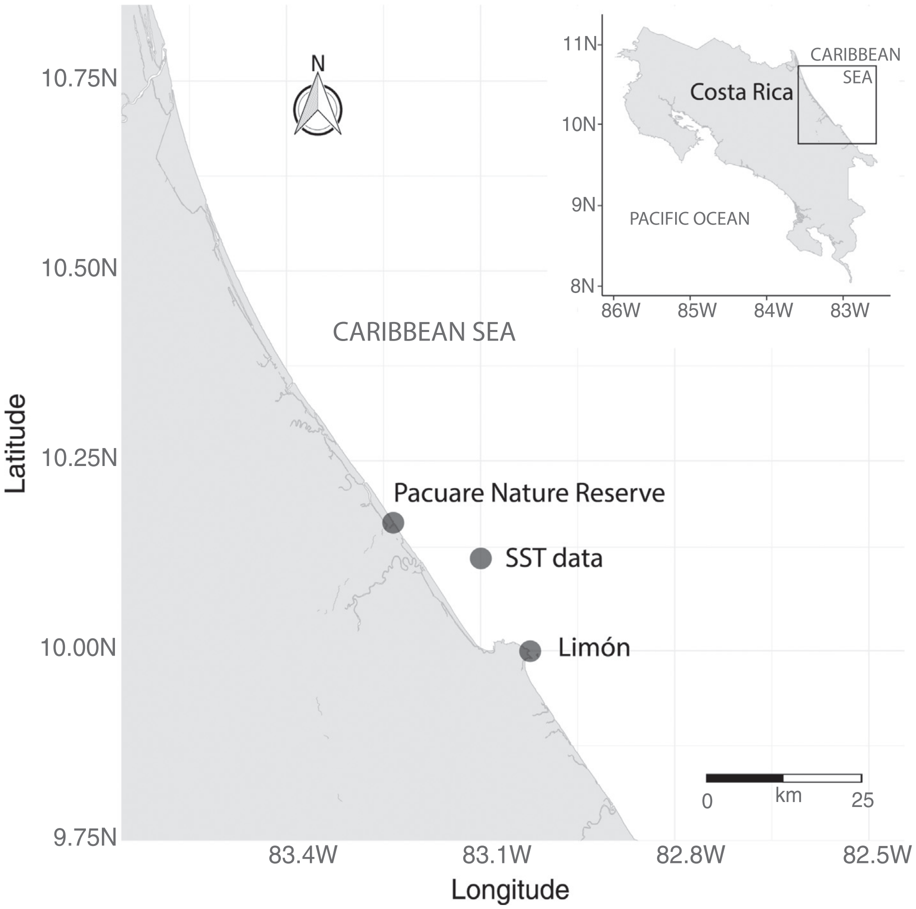

Fig. 1. Location of the monitoring beach at Pacuare Nature Reserve, on the Caribbean coast of Costa Rica.

3. Results

The six nesting seasons included in our analyses had a sum of 773 days with nesting activity, in which a total of 6770 nests and 4591 aborted attempts were reported. The highest values recorded per night were 32 nests and 19 aborted attempts, with an average of 5.9 ± 5.2 and 2.8 ± 2.9 (mean ± SD), respectively. We found a moderate degree of correlation between the variables (Pearson correlation $r = 0.55$, $P < .0001$) (Fig. 3). The dispersion of the data suggested that, although nights with high numbers of nests tend to show higher number of aborted attempts, other factors may influence having a night's success, with more nests than aborted attempts.

The selected model showed which environmental conditions make successful nesting likely to happen, presented an AICc value of 2551.3 and contained a lower number of parameters than other competing models (Table 1). The model yielded positive relationships between the probability of having successful nesting and barometric pressure (GLMM test, $z = 3.617$, $p < .001$) and wind speed (GLMM test, $z = 2.297$, $p < .05$), in order of importance. The relationship between successful nesting and low and high tides was negative (low tide: GLMM test, $z = -3.518$, $p < .001$; and high tide: GLMM test, $z = -2.599$, $p = .01$), in order of importance (Table 2). Wind

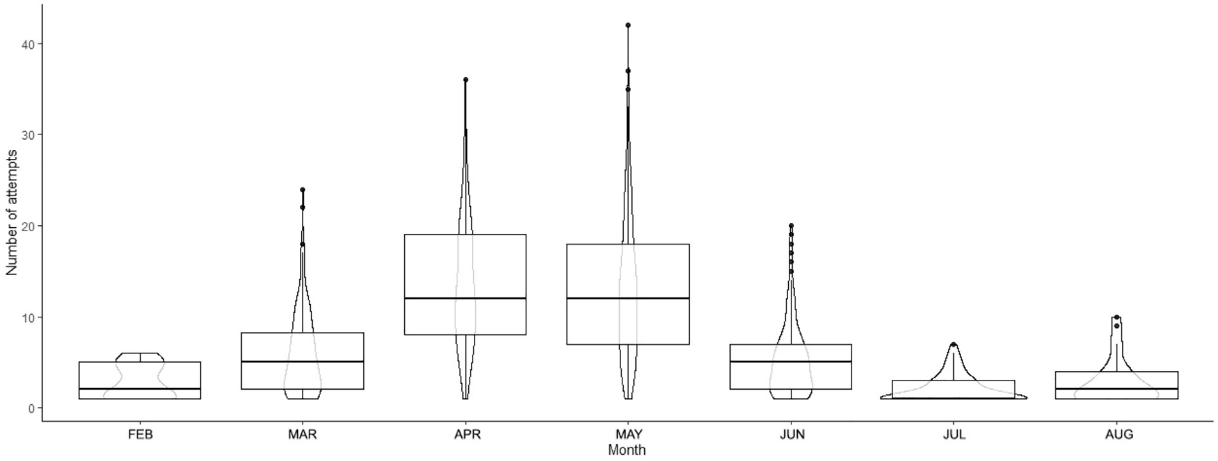

Fig. 2. Seasonal nesting cycle at Pacuare Nature Reserve from 2010 to 2015. The y-axis combines both nests and aborted attempts per night.

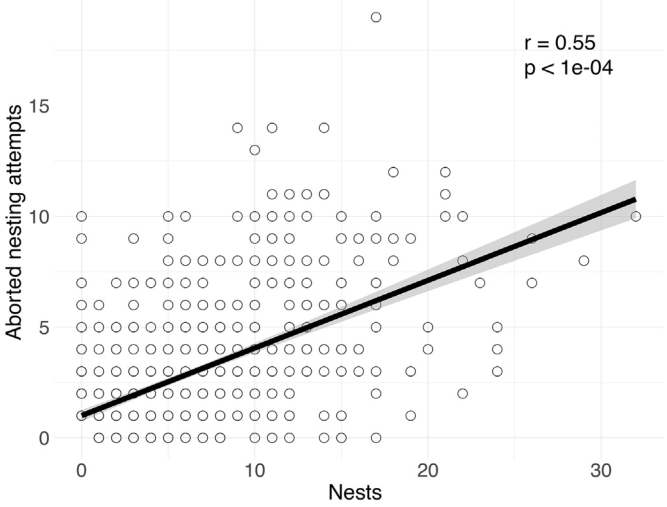

Fig. 3. The relationship between successful nesting attempts and aborted attempts. Data from nesting seasons 2010 to 2015 at Pacuare nesting beach, Costa Rica.

Table 2
Results of the selected model. Wind speed, barometric pressure, low tide and high tide were standardized.

	Estimate	Std. Error	z value	*p*-value
Intercept	0.760	0.147	5.180	0.000
Wind speed	0.086	0.037	2.297	0.022
Pressure	0.128	0.036	3.617	0.000
Low tide	−0.127	0.036	−3.518	0.000
High tide	−0.098	0.038	−2.599	0.009

direction, as a random effect with 8 levels, yielded variance 0.022 and standard deviation (SD) 0.148. Year showed variance 0.095 and SD 0.308, and Julian day yielded variance 0.166 and SD 0.407. We plotted all data in order to visualize the relationship between the variables included in the model and the number of nests and aborted attempts. Correlations are in general rather weak due to high dispersion of the environmental data, but some trends can be observed. Wind speed is positively correlated to nests and barometric pressure has a negative correlation with aborted attempts. Out of all tidal data, low tide shows the strongest negative correlation with nests. Rain was not included in the selected model, but it was included in the model with the lowest AIC value. We plotted the data in order to detect any trends and we observed that the highest rainfall values are related to both low number of nests and aborted attempts (Fig. 4).

4. Discussion

The understanding of a species reproductive behaviour is crucial for their conservation management (Mazaris et al., 2004; Mazaris et al., 2008). It has been widely suggested that sea turtles follow environmental cues, both atmospheric and oceanic, to emerge from the sea in order to lay their clutches (Barik et al., 2014; Schofield et al., 2010), although there is still uncertainty about the specific factors driving nesting activity (Frazer, 1983; Bowen et al., 2005). The motivation of this study was, therefore, to increase the knowledge about the reproductive behaviour of these marine reptiles.

To address this issue, we analysed the effect of a series of environmental factors on both the number of nests laid per night and the number of aborted attempts. The correlation between nesting activity and wind and barometric pressure was positive. Results from the GLMM showed a negative correlation between the nesting success and both high and low tides. This is consistent with previous findings (Pike, 2008) on loggerhead turtle (*Caretta caretta*) nesting in Florida, although it contradicts the widespread thought that high tides favour nesting. A significant preference for loggerheads to nest during the highest tidal stages was found in Georgia, USA (Frazer, 1983). Frazer (1983) suggested that these differences are due to the amplitude of the tidal regime. In that case, areas with diurnal tides (wider range) show the positive influence of high tides on nesting, while in places with semidiurnal tides (with a narrower range, such as Florida and Caribbean Costa Rica), high and low tides tend to have a negative effect on nesting. This indicates that other tide-related factors, such as tidal currents, could be influencing negatively turtle emergences. It has been hypothesized that turtles start their nesting season when certain environmental thresholds are reached (Bowen et al., 2005) and randomly emerge to lay their clutches throughout the season. However, we found that nests and aborted attempts were not strongly correlated, suggesting that some nights were more suitable for nesting than others. Katselidis et al. (2013) and Pike (2008) have also found differences in factors driving nesting and aborted attempts. Particularly, Pike (2008) found that higher barometric pressure influenced positively the successful nesting activity for loggerhead turtles, which is consistent with our results. Other hypotheses suggest that turtles could follow different cues during emergence and during nest site selection (Wood and Bjorndal, 2000; Pike, 2008). These factors could be environmental, as our results showed, or abrupt changes in beach physical characteristics, as other studies have found (Godley et al., 2001; Weishampel et al., 2003; Mazaris et al., 2006; Rivas et al., 2016a). Dodd (1988) identified an influence of rainfall in nesting, and we observed that the highest values of rainfall were correlated to low numbers of nests and aborted attempts. In adittion, heavy rainfall is known to affect nest conditions, e.g. by lowering sand temperature (Lolavar and Wykenen, 2015; Rivas et al. 2019). Neither maximum nor minimum air temperatures were included in the selected model, suggesting that their capacity to explain differences in nightly nesting activity is fairly poor. However, maximum temperatures are likely to determine the timing of the nesting season (Godley et al. 2001) and, in temperate areas, they even seem to define the end of the nesting season (Katselidis et al. 2012). The effect of sea surface temperature has been widely stated as a factor driving nesting in temperate areas (Hays et al. 2002; Mazaris et al. 2004). In tropical areas, however, average temperature remains around 27 °C and barely varies throughout the year. High and low tides are also dissuading nesting, which suggests that turtles can notice when tidal cycles reach their extremes and avoid their effects, as pointed by Kamel and Mrosovsky 2004). At lower tides, emergence can be too energetically demanding for this heavy-weighted turtles species (Wallace and Jones,

Table 1
Model selection table, with all candidate models ranked according to AICc values. The selected model is shown in bold.

Intercept	High tide	Low tide	Pressure	Rain	T.max	T.min	SST	Wind speed	df	AICc
0.756	−0.100	−0.131	0.136	−0.072				0.081	9	2549.6
0.759	−0.099	−0.136	0.112	−0.064		−0.048		0.077	10	2550.5
0.759	−0.096	−0.137	0.116	−0.071			−0.045	0.083	10	2550.5
0.763	−0.097	−0.135	0.098			−0.063		0.081	9	2551.3
0.760	**−0.098**	**−0.127**	**0.128**					**0.086**	**8**	**2551.3**
0.755	−0.099	−0.128	0.144	−0.066	0.021			0.075	10	2551.4

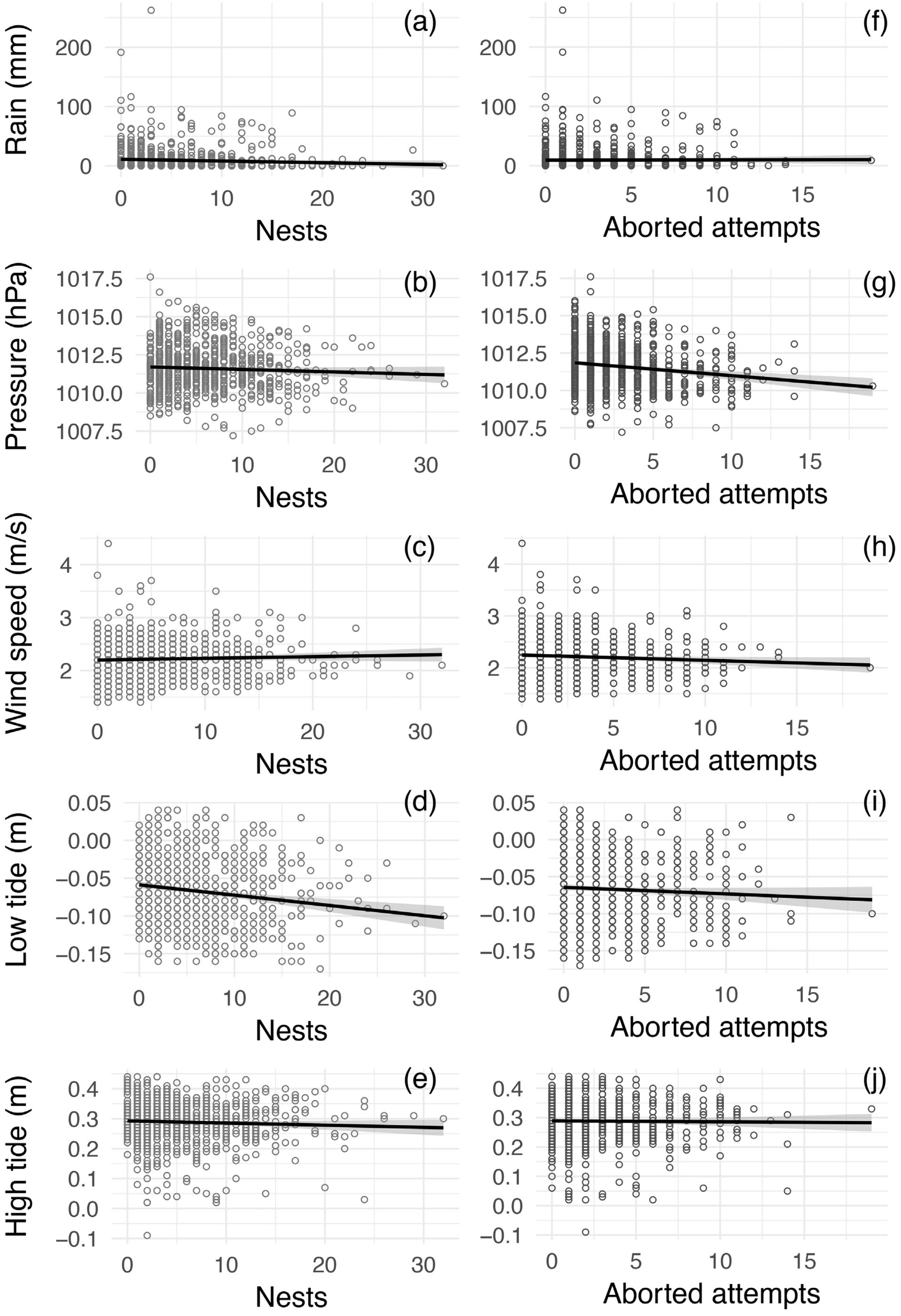

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Fig. 4. Regression plots showing the relationship between environmental predictors and nesting variables at Pacuare nesting beach. On the left column, nests vs. rainfall (a), barometric pressure (b), wind speed (c), low tides (d) and high tides (e). On the right column, number of aborted attempts vs. rainfall (f), barometric pressure (g), wind speed (h), low tides (i) and high tides (j).

2008). Climatic features related to local precipitation (Santidrian-Tomillo et al., 2015), storm episodes and heavy rainfall (Rivas et al. 2018) may influence the nesting behaviour of leatherback turtles. If environmental data had been collected on the same study site (Fig. 1), or if the temporal resolution had been higher, perhaps the model would have detected stronger rainfall effects. It has been previously reported that sea turtles tend to nest on beaches that are more exposed to wind and wind-generated waves (Santana Garcon et al. 2010). In this way, wind conditions seem to influence nesting selection of adult turtles, thus suggesting that changes in wind patterns might also affect turtle nesting behaviour.

Therefore, and taking into account the increase in both frequency and intensity of storm episodes in tropical areas since the 1990s (Goldenberg et al. 2001; Patino-Martinez et al. 2014), our findings suggest a likely negative effect on leatherbacks' nesting activity, which could ultimately represent an additional obstacle to the reproduction of this threatened species. Vulnerability assessments have drawn similar conclusions for other sea turtles globally (Katselidis et al. 2014; Fuentes et al. 2011).

We recommend replicating this study for other leatherback populations as well as for other species of marine turtles. Global overview on the climatic and oceanographic cues driving nesting, and how climatic variations could threaten sea turtle populations in the near future. These findings, combined with reliable nest site selection information, could represent an important tool for the management strategy of conservation projects.

Research data policy

The datasets during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Declaration of Competing Interest

Author A declares that he has no conflict of interest. Author B declares that he has no conflict of interest and Author C declares that she has no conflict of interest.

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CLIMATE CHANGE AND SEA TURTLE NESTING

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RESEARCH ARTICLE

Predicting the impacts of sea level rise in sea turtle nesting habitat on Bioko Island, Equatorial Guinea

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Abstract

Sea level is expected to rise 44 to 74 cm by the year 2100, which may have critical, previously un-investigated implications for sea turtle nesting habitat on Bioko Island, Equatorial Guinea. This study investigates how nesting habitat will likely be lost and altered with various increases in sea level, using global sea level rise (SLR) predictions from the Intergovernmental Panel on Climate Change. Beach profiling datasets from Bioko's five southern nesting beaches were used in GIS to create models to estimate habitat loss with predicted increases in sea level by years 2046–2065 and 2081–2100. The models indicate that an average of 62% of Bioko's current nesting habitat could be lost by 2046–2065 and 87% by the years 2081–2100. Our results show that different study beaches showed different levels of vulnerability to increases in SLR. In addition, on two beaches erosion and tall vegetation berms have been documented, causing green turtles to nest uncharacteristically in front of the vegetation line. We also report that development plans are currently underway on the beach least susceptible to future increases in sea level, highlighting how anthropogenic encroachment combined with SLR can be particularly detrimental to nesting turtle populations. Identified habitat sensitivities to SLR will be used to inform the government of Equatorial Guinea to consider the vulnerability of their resident turtle populations and projected climate change implications when planning for future development. To our knowledge this is the first study to predict the impacts of SLR on a sea turtle nesting habitat in Africa.

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Introduction

One of the important discussions involving climate change and sea turtle conservation is the imminent loss of sea turtle nesting habitat in relation to increasing sea level rise (SLR) [1, 2, 3]. The Intergovernmental Panel on Climate Change (IPCC) has generated four scenarios that predict SLR for years 2046–2065 and 2081–2100 [4]. The IPCC indicates that an increase of about 44 to 74 cm will be experienced globally by the year 2100, which will have previously un-

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investigated implications for the second largest nesting aggregations of leatherback (*Dermochelys coriacea)* and green sea turtles (*Chelonia mydas*) in West Africa [4–8]. Due to low elevations and limited capability for shoreline retreat, small islands are at the greatest risk from climate change [9, 10], and expected effects include increased salinity within the water table, beach erosion, and sand inundation with increased tide elevation [11, 12].

Marine reptiles have evolved with natural coastal erosive processes such as high-tide flooding, accretion, and seasonal erosion, but the extreme beach modification of the past half-century is progressing at a rate faster than the rate at which some species can adapt [1]. The Great Barrier Reef green sea turtle nesting population, the largest in the world, has experienced hatchling success reduction in the past few years, which is thought to be a result in part of a rising groundwater table [13]. It has been estimated that the most extreme SLR predictions will result in inundation of 27 percent of Great Barrier Reef green sea turtle nesting habitat [3]. Nesting habitat inundation is also expected in other nesting sites around the world, including Bonaire (26%) and Barbados (32%) with a 0.5 m rise in sea level [1, 2].

For nesting habitat that is not inundated, SLR will likely alter the potential for previous nesting beaches to continue to maintain their historic turtle reproductive output [1]. With an overall reduction in nesting habitat, if the rate of shoreline retreat continues to lag behind that of beach erosion, the density of nests will likely increase within the area of available nesting habitat. This has potential to cause decreased hatching success through increased contamination and physical disturbance of nests by co-specifics [2, 13–16]. Since sea turtle species can shift their nesting grounds when faced with unsuitable nesting habitats [17–20], it is important to also investigate multiple nesting areas within a nesting region [3]. It has been suggested that with 0.48 m SLR in the Hawaiian Islands, green sea turtle nesting localities will likely need to shift primarily from Trig, Gin, and Little Gin islands to East Island in order for historic reproductive productivity to be sustained [21]. With increasing SLR, increases in erosion rates and nests that are flooded from storms can be expected [10, 22, 23]. Effects from an increased water table due to SLR can already be observed on Raine Island, Australia, where depressions from sea turtle body pits have been observed filling with water [13, 24]. This increased nest inundation will likely cause decreases in reproductive output of all sea turtle species [13].

The 10.75 km of main sea turtle nesting beaches (Fig 1A–1E,) on the southern side of Bioko Island are critically important nesting habitat for the leatherback and green sea turtles in the West/Central African region [8, 25–27]. Further genetic analyses and internesting satellite tracking studies for green and leatherback turtles in the Gulf of Guinea are required to further understand the fidelity of turtles to Bioko Island and the potential for Bioko nesting turtles to be part of the same populations observed in Gabon and Congo [8]. On Bioko green turtles nest mostly on beaches A, B and C, and leatherback sea turtles on C, D and E [8]. Within and among species, there is variation in selection for more specific beach characteristics such as beach length, width, height, slope, orientation, and vegetation [28–31]. The various beach types where sea turtles nest combined with the specific nest-site characteristics that are selected for by each species can be altered in diverse ways by increasing sea level [1]. Green turtles prefer to nest on narrower, steeper beaches and in the area behind the vegetation line, whereas leatherback sea turtles prefer wider, flatter beaches and the area between the high tide line (HTL) and the vegetation line [32, 33]. It has been found previously that narrower beaches at lower elevations are more susceptible to SLR [1]. As the morphology of the beaches and intricate beach zoning is altered, these habitat selection differences cause species-specific SLR threats. Based on the spatial distribution of nests within each species, the threat from nest inundation could be more severe and more imminent for some species than others.

The goal of this study is to characterize sea turtle nesting beaches on Bioko Island and to model the effects of SLR for use in generating targeted conservation management plans. Nest

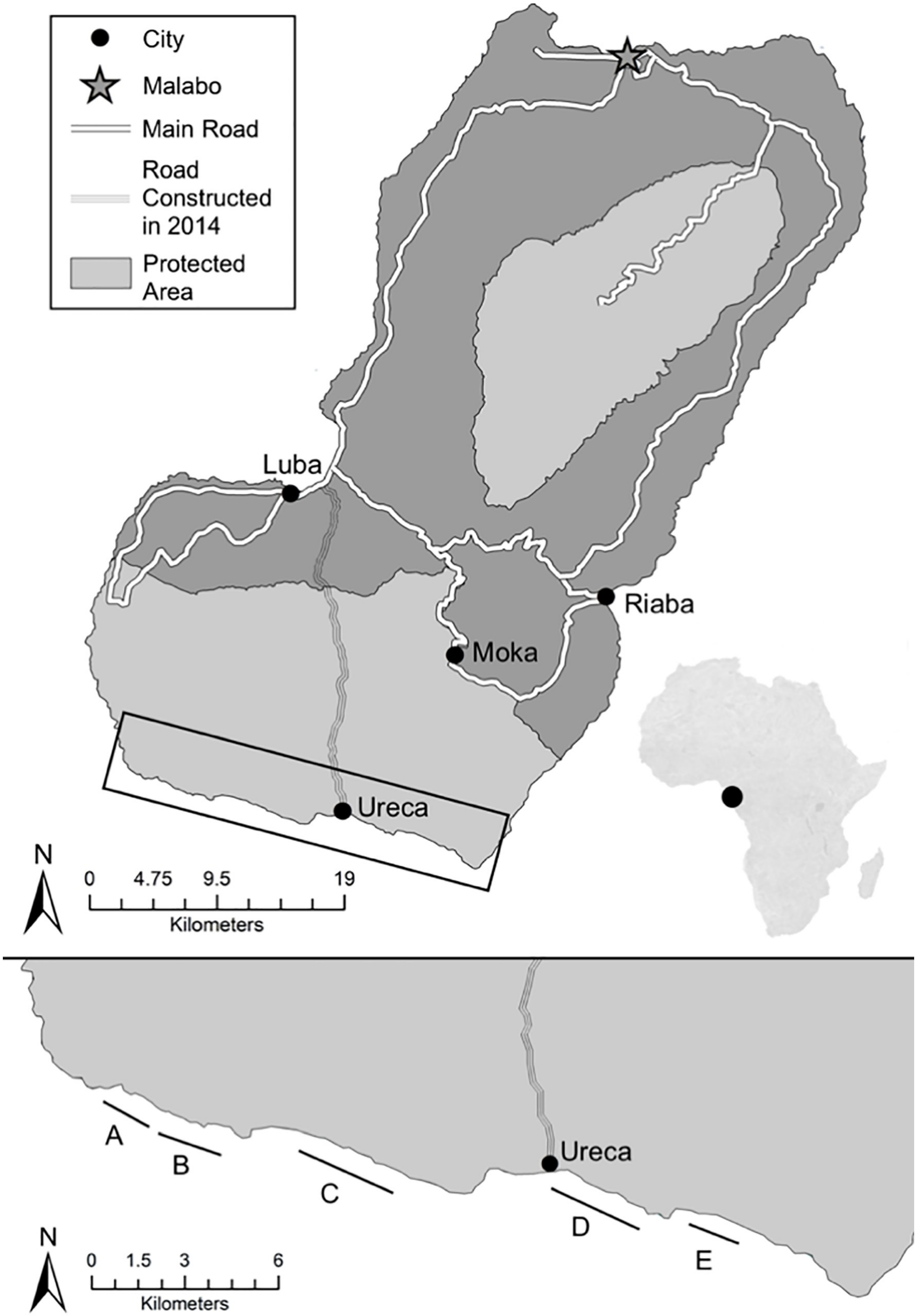

Fig 1. Bioko Island nesting beaches. The five nesting beaches are labelled with letters A–E.

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Table 1. Beach morphometrics of Bioko's five turtle nesting beaches 1.

Beach	Length (km)	Total Area (m^2)	Current Nesting Habitat (m^2) (Proportion of Total Beach Area)
A	1.7	84,914	8,852 (0.10)
B	1.9	145,350	10,350 (0.07)
C	2.9	236,784	23,946 (0.10)
D	2.65	350,564	63,592 (0.18)
E	1.6	153,110	16,217 (0.11)

Morphometrics of Bioko's five nesting beaches. Nesting habitat is defined as the area between the high tide line and vegetation line.

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locations from both green and leatherback turtles were used together with SLR predictions on Bioko's 5 nesting beaches to determine how each species will likely be affected in the upcoming decades by climate change. Our objectives were to (1) construct a 3D profile of 5 nesting beaches by collecting morphometric/contour data in an x, y, z dimensional space, (2) use triangulated irregular network models and digital elevation models to map landward movement of the HTL, and (3) predict how the model output will affect green and leatherback turtle nesting on Bioko Island.

Materials and methods

Data collection

Beach profiling transects were conducted on all five of Bioko's nesting beaches (A-E) (Fig 1, Tables 1 and 2). Beach characterization methods were consistent with a similar SLR prediction model for 13 beaches on the island of Bonaire, Dutch Antilles [1]. The profile of each beach was recorded at 50 m intervals along the beaches using a 60 m measuring tape. The transects on each beach were 50 m apart, perpendicular to the water line, and spanned the distance from the vegetation line to the drop off during lowest tide. A meter tape, compass and Abney level, a surveying instrument consisting of a sighting tube, movable spirit level and protractor scale, were used to create profiles of beach topography and dimensions at each change in slope along the transect [2]. Accuracy to ground truth was relative to the stake GPS point (Garmin GPSMap 64) at the start of each transect. To ensure maximum accuracy, up to 6 different waypoints for the same stake on each beach were averaged to generate an average stake reference point to be used in the following spatial analysis. During the process of beach profiling, the location of the high tide line was indicated. Three times throughout the nesting season, the high tide line of all beaches was walked to create a GPS track that could then be used in conjunction with the HTL identified during profiling to standardize the average location of the

Table 2. Beach morphometrics of Bioko's five turtle nesting beaches 2.

Beach	Max. Elevation (m)	Min. Elevation (m)	Average Elevation (m)	Max Width (m)	Min Width (m)	Mean Width (m) ±SD
A	1.78	-5.23	-2.50	100.23	16.9	49.06 ± 14.87
B	1.85	-4.51	-2.64	158.24	9.68	70.67 ± 31.03
C	1.86	-3.46	-2.40	137.14	29.44	78.80 ± 23.65
D	1.77	-2.83	-1.61	215.49	81.3	126.076 ± 31.70
E	1.30	-3.00	-2.40	154.65	59.93	94.80 ± 18.15

Morphometrics of Bioko's 5 nesting beaches based on 2017 profiling data. Averages show ± standard deviation.

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high tide line for modelling purposes. Beach D was profiled once at the beginning of the season and once at the end to better understand how seasonal fluctuations could affect SLR predictions for a single beach. The circular error probable for each stake was calculated. This work was conducted under appropriate permits from Universidad Nacional de Guinea Ecuatorial (#289/2016) and the Institutional Animal Care and Use Committee at Purdue University (IACUC protocol #1410001142).

This study was conducted from October 2016 through February 2017, coinciding with the leatherback and green sea turtle nesting season on Bioko Island. During nightly beach patrols or morning walks, nest and false crawl locations for every leatherback and green sea turtle encountered on Beach C (2.9 km) and D (2.5 km) were recorded using GPS (Garmin GPSMap 64). To understand the adaptability of sea turtle behavior in the face of changing available nesting habitat, part of the data collection throughout the nesting season included the nest abortion behavior of the females in their search to find suitable nesting habitat. At all nesting sites and every time a nesting attempt was aborted, data such as GPS point, beach zone, and distance to the high tide and vegetation lines was collected. Turtles entangled in vegetation during morning walks were freed.

Spatial analysis

A program was written in Python to generate a waypoint and elevation at each change in slope on the transects and at the present elevation of the high tide line. In ArcMap (Esri version 10.4), GPS points with their respective elevation values were entered as x, y, z data and then projected as shapefiles. All elevations were relative to the HTL, which for the purposes of this project is at an elevation of 0 m. The weighted average elevation of each beach was determined by utilizing the average elevation and length of all transect segments. The vertical error of each profile segment was determined using the generally accepted measurement error of the Abney level (4.31%) [34]. The total error of each profile was determined by adding the sequence of vertical errors along the profile in quadrature. The average vertical error of all profiles was determined to be 0.074 m ± 0.027 (standard deviation). The “points to line” feature in ArcMap was used to create five lines connecting: 1) stake GPS points, 2) HTL GPS points, 3) GPS points of the final segment of each transect, 4) GPS points for transect 1 on each beach, and 5) all points on the last transect for each beach. These lines allowed the “feature to polygon” tool to be used to create two polygons of each beach, one delineating the area between the HTL and vegetation line and another delineating the area between the final segment of each transect (at the beach dropoff visible at low tide) and the vegetation line. Total beach area was determined by calculating the area of the polygon between the vegetation line and the beach drop off at low tide. Available nesting habitat was determined by calculating the area of the polygon between the high tide line and vegetation line. The proportion of the total beach area that is available for nesting was calculated by dividing the area of available nesting habitat by the total beach area. To model sea level rise, the waypoints from all changes in slope on all transects were then used as inputs to the “topo to raster” tool to create a digital elevation model, which is an array of regularly spaced elevation values referenced horizontally. The raster dataset was then used in the creation of a triangulated irregular network model, for 3D visualizations of beach morphology and changes due to SLR [1, 3] (S1 Fig). The raster datasets were projected and reclassified to reflect the IPCC sea level rise projections (0.24, 0.25, 0.26, 0.30, 0.4, 0.48, 0.63 and 0.75 m) [4] (Tables 3 and 4). The range of one class of each raster always ended at 0 m, so the current approximate viable nesting habitat could be easily isolated. The “extract by mask” feature was then used to clip these rasters to the polygons of each beach. The count of each class along with the cell size was used to calculate the area of each beach, area of current

Table 3. Habitat loss projections on turtle nesting beaches under 4 IPCC scenarios for 2046–2065.

	Nesting Habitat Inundated (proportion of total nesting habitat)				
Beach	**0.24 m**	**0.25 m**	**0.26 m**	**0.30 m**	**Mean**
A	6,209 (0.70)	6,344 (0.72)	6,444 (0.73)	6,835 (0.77)	0.73
B	8,507 (0.78)	8.633 (0.79)	8,760 (0.80)	9,282 (0.85)	0.81
C	13,422 (0.50)	13,851 (0.52)	14,245 (0.53)	15,802 (0.59)	0.54
D	29,246 (0.45)	30,092 (0.46)	30,938 (0.48)	34,522 (0.53)	0.48
E	9,404 (0.50)	9,807 (0.52)	10,151 (0.53)	11,373 (0.60)	0.54

The potential area (m^2) on 5 of Bioko's nesting beaches that would be lost to sea level rise.

(SLR) under 4 scenarios for 2046–2065: 0.24, 0.25, 0.26, and 0.30 m. The average represents an average SLR loss predicted by the 4 scenarios for 2046–2065. Quantities in parentheses represent the nesting habitat inundated under each scenario as a proportion of the total nesting habitat.

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nesting habitat, and area lost and left under each SLR predation. This type of model is consistent with "bathtub" modelling and does not take into account future shoreline retreat. ArcScene (Esri version 10.4) was used to create 3D graphics of models, and ArcGIS software was used to generate all maps and basemaps. Species-specific predictions of impacts of climate change were then made based on the spatial presence (i.e. nest locations relative to vegetation and high tide lines) of each species on each beach coupled with the beach's vulnerability to SLR.

Results

The average circular error probable for the reference points was 2.43 m ± 1.44 (standard deviation), indicating that 2.43 m is the radius of a circle centered around the mean position of each reference stake that contains 50% of the reference stake GPS points. Similarly, the circular error probable was 3.85 m ± 2.51 (standard deviation) for 98% of the reference stake GPS points. Projections in GIS of the reference points and transects confirmed their proper spacing and alignment.

Beach A is the smallest beach with an average beach width of 49.06 m and a total beach area of 84,914 m^2 (Tables 1 and 2). Beach A also had the smallest area of nesting habitat in 2017, 8,852 m^2, but Beach B has the smallest percentage of nesting habitat to total beach area, 7% (Table 1). Beaches C and D were the two longest and widest nesting beaches on Bioko Island, with areas of 236,784 m^2 and 350,564 m^2, respectively (Tables 1 and 2). Beach D contained the highest percentage of nesting habitat out of all 5 beaches, 18% (Table 1). Satellite imagery and

Table 4. Habitat loss projections on turtle nesting beaches under 4 scenarios for 2081–2100 and 1 scenario for 2100.

	Nesting Habitat Inundated (proportion of total nesting habitat)				
Beach	**0.4 m**	**0.47 m**	**0.48 m**	**0.63 m**	**0.75 m**
A	7,544 (0.85)	7,851 (0.89)	7,887 (0.89)	8,239 (0.93)	8,396 (0.95)
B	9,576 (0.93)	9,960 (0.96)	9,996 (0.97)	10,296 (0.99)	10,338 (1)
C	18,282 (0.76)	20,052 (0.84)	20,280 (0.85)	22,494 (0.94)	23,328 (0.97)
D	42,782 (0.67)	47,314 (0.74)	47,885 (0.75)	54,761 (0.86)	58,542 (0.92)
E	12,761 (0.79)	13,723 (0.85)	13,722 (0.85)	15,313 (0.94)	15,869 (0.98)

The potential area (m^2) on 5 of Bioko's nesting beaches that would be lost to sea level rise (SLR) under 4 scenarios for 2081–2100: 0.4, 0.47, 0.48, and 0.63, and 1 scenario for 2100, 0.75 m. The mean represents an average SLR loss predicted by the 4 scenarios for 2081–2100. Quantities in parentheses represent the nesting habitat inundated under each scenario as a proportion of the total nesting habitat.

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photographs showed the evident discrepancy across nesting beaches in terms of nesting habitat available in 2017 (S2 Fig). The average elevation relative to the high tide line of Beach B was the lowest (-2.64 m) and that of Beach D the highest (-1.61 m) (Table 2). Beach A was the steepest beach with a slope of 0.086, and Beach D was the shallowest with a slope of 0.022. Beach A was the only beach that had a significantly different slope than all other beaches. The error of the elevation measurements, or the vertical error, was 0.043 m ± 0.016 (standard deviation).

There are four scenarios from the Intergovernmental Panel on Climate Change (IPCC) that predict SLR for years 2081–2100 and for the years 2046–2065. The results presented here are calculated with average SLR under Representative Concentration Pathways (RCP) 2.6, 4.5, 6.0, and 8.5 for 2081–2100, the average SLR under RCP2.6, 4.5, 6.0, and 8.5 predictions for 2046–2065, and the average SLR under the RCP8.5 prediction specifically for 2100. The RCP8.5 prediction for 2100 was included to show the most extreme extent of current IPCC predictions.

Within only 30 years, using different scenarios of SLR, these models predict changes in nesting habitat availability. Under the most extreme scenario for 2046–2065, with a 0.3 m increase in sea level, Beach D is predicted to lose the least amount of its current nesting habitat, only 53%, and Beach B is expected to lose the most with a predicted 81% nesting habitat loss (Table 3). Under the least extreme scenario, all beaches will lose at least 45% of its current nesting habitat, and Beach B is likely to lose 78% of its current available nesting habitat (Table 3). Based upon the habitat loss predictions exhibited in Table 3, the beaches where green sea turtles nest in greater quantities, A and B, will experience higher nesting habitat losses than those where leatherback sea turtles nest more often, D and E (Table 3). Under the least severe scenario, the largest proportion of current nesting habitat that would be left by 2046–2065 was 55% on Beach D, and the smallest proportion of nesting habitat that would remain on Beach B is 22% (Table 3).

Under the RCP8.5 predictions for SLR in year 2100, all beaches were predicted to lose at least 92% of their current nesting habitat (Table 4). For the average SLR across RCP2.6, 4.5, 6.0 and 8.5 scenarios for 2081–2100, no beach was predicted to lose less than 67% (Table 4). Under the most extreme scenario, Beach B is predicted to be completely inundated (Table 4). The beach expected to lose the least amount of nesting habitat is Beach D with a predicted 92% loss by the year 2100 (Table 4). Beach D is the largest and widest beach and also has the highest minimum elevation and highest average elevation of any nesting beach on the south side of the island (Tables 1 and 2). The total area across all five nesting beaches that is predicted to remain on Bioko Island for nesting under the most extreme scenario is about 6,428 m^2, which is only about 5.23% of the nesting habitat currently available. Under the least extreme scenario, approximately 31,998 m^2 of nesting habitat is likely to be viable, 26.02% of current habitat estimates (Table 4). Beaches typically characterized as green sea turtle nesting habitat (Beaches A, B, and C) face an average of 90% nesting habitat loss for 2081–2100, and those of leatherback sea turtles (Beaches C, D and E) face an average loss of 82% (average of 0.4, 0.47, 0.48, and 0.63 m predictions).

Beach D was profiled twice within the same season, and the results show how these predictions could fluctuate. The first time the analysis was conducted with the first set of data, the maximum predicted habitat loss for Beach D was 91.84%. The second analysis, conducted with the second set of data, revealed a habitat loss of 92.06%. This is a percent difference of 0.24% and is considered negligible for this study's specific objectives.

Narrower, steeper and less elevated beaches appear to be more vulnerable to climate change. Although there was a negative correlation between increasing beach elevation and average nesting habitat loss, the relationships between maximum ($F = 0.24$, $df = 1,3$, $R^2 = 0.66$, $p = 0.66$), minimum ($F = 7.23$, $df = 1,3$, $R^2 = 0.71$, $p = 0.075$) and average elevation (m) ($F = 6.13$, $df = 1,3$, $R^2 = 0.67$, $p = 0.090$) with average nesting habitat loss (proportion of current

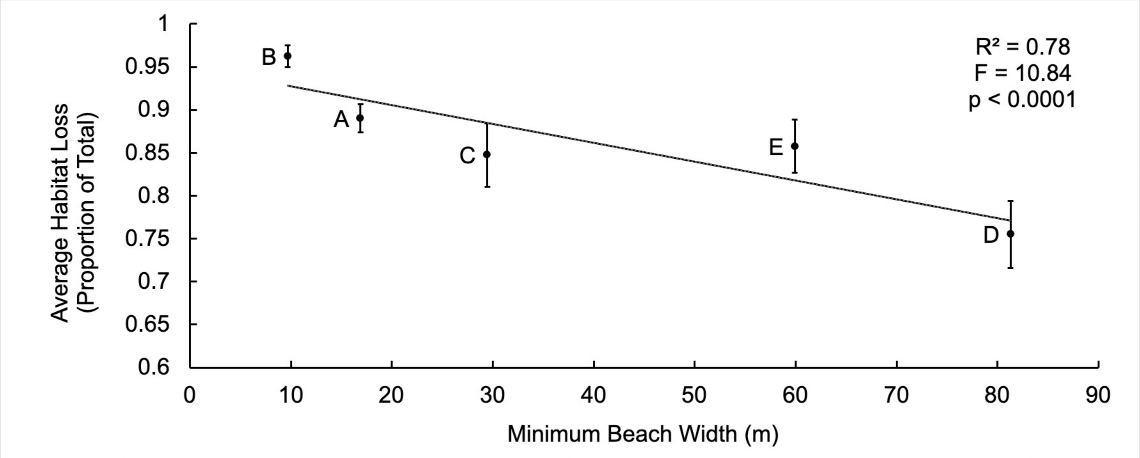

Fig 2. Minimum beach width versus average habitat loss. Relationship between minimum beach width (m) and average habitat loss (proportion of whole). Error bars are standard error from the mean.

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total nesting habitat) were not significant. The five nesting beaches did not have significantly different elevations (F (4,1327) = 2.01, p = 0.092). The data shows significant negative relationships between minimum beach width (Fig 2) with average habitat loss (proportion of current total nesting habitat). As the beaches become wider, the average habitat loss decreases. A significant positive relationship between average slope and average habitat loss was observed (Fig 3). Beach D, the beach expected to lose the least of its current nesting habitat, has the flattest slope and the highest minimum elevation (Table 2). During the spring high tide during the full moon in November 2016, there was no distance between the HTL and vegetation line [31]. Green turtle nests were laid in steeper and narrower sections of the beach, whereas leatherback nests were laid in shallower and wider areas (Fig 4).

Threats of nest inundation, predation, and entanglement were identified and uncharacteristic green turtle nesting at the high tide line and in front of the vegetation line in the presence of vegetation berms was documented. With rapid beach erosion on narrow beaches, steep

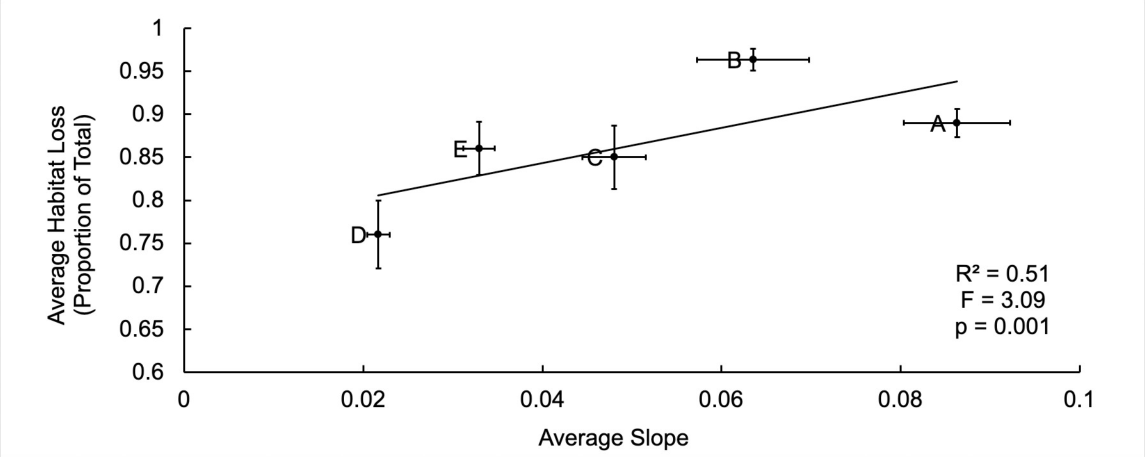

Fig 3. Average beach slope versus average habitat loss. Relationship between the average slope on beaches A, B, C, D, and E and their average expected habitat loss (expressed in proportion of whole nesting habitat currently available). The averages are for scenarios 0.4, 0.47, 0.48, and 0.63 m for years 2081–2100. Error bars are standard error from the mean.

https://doi.org/10.1371/journal.pone.0222251.g003

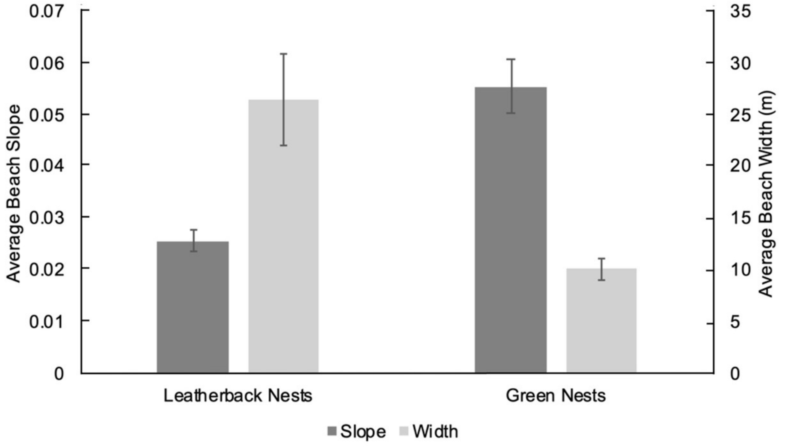

Fig 4. Leatherback and green turtle species specific nest site selection based on beach slope. Mean beach slope and width for 24 leatherback and 11 green clutches on Beaches C & D. Error bars are standard error from the mean.

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vegetation berms, where the high tide and vegetation lines are one in the same, are left as evidence that the rate of shoreline retreat lags behind that of beach erosion. Green turtles often struggle to reach the vegetation line, as they are unable to surmount steep vegetation berms or become entangled in overhanging root systems where the sand has eroded away beneath (Beach A). Green sea turtles are being found in dangling root matrices with increasing frequency on Beaches A and B (Honarvar, *personal observations*). Instead of surmounting vegetation berms, green turtles on Beaches A and B have been observed nesting in front of the vegetation and along the high tide line, where their nests are at an increased threat from tidal inundation. In other areas scattered along Bioko's nesting beaches, classic beach zoning between the high tide line and vegetation is nonexistent but no berms are present, causing the waves to lap against the trees. In these flatter areas, more characteristic of leatherback nesting beaches, like Beaches D and E, leatherback turtles seeking dry sand to lay their eggs can be found stuck in between the trees. Furthermore, a leatherback turtle was discovered with a tree stuck in between her shoulder and neck, causing immobilization. Turtles emerge from the surf in search of dry sand to lay their eggs and instead enter the forest.

Data from standard monitoring efforts during the 2016/17 nesting season documented 284 combined night patrol and morning walk leatherback encounters and showed that 89% (n = 26) of the time when a leatherback was found digging her nest below the HTL and the nest filled with water, she aborted that nest to choose a drier location closer to the vegetation.

Discussion

As beaches erode, beach morphological changes produce species specific threats to sea turtles as they select for suitable sites to lay their eggs. Our results suggest there is a link between minimum beach width and average habitat loss (Fig 2, $F = 10.84$, $R^2 = 0.78$, $p<0.0001$) as well as average slope and average habitat loss (Fig 3, $F = 3.09$, $R^2 = 0.51$, $p = 0.001$) based on five data points (five beaches). More work is needed to confirm these preliminary results. The behavior of green turtles to select for narrower, steeper beaches to nest could put them at a greater risk to climate change than other turtle species, as the beaches where they characteristically nest may be morphologically predisposed to erode first based upon the data presented here. Large-scale nest inundation and increased nest conductivity, an indication of moistness due to saltwater inundation, is being observed for this species on Beaches A and B and is expected to continue [35]. Nesting in front of the vegetation line to avoid stark vegetation berms and increased nest conductivity are quantifiable changes within green nesting habitat and nest selection that require further investigation to determine their effects on hatching success and hatchling production. At this time, we expect that increased inundation risk will result in increased nest mortality, and increased sand conductivity will be a significant negative influence on hatching success [35]. At present while nesting habitat still largely remains on Bioko's nesting beaches, leatherback turtle nest site selection behavior, in nesting closer to the HTL and in front of the vegetation line, generally puts the nests of this species at a greater risk to tidal inundation regardless of the morphology of the beach they are nesting on [35]. As sea level rises and beach erosion progresses, however, potentially eroding steeper and narrower beaches first and causing unsurmountable berms along the vegetation line, green turtles may be first to lose their nesting beaches altogether.

The results presented here represent passive flooding scenarios and the threat of coastal squeeze, which occurs when beaches are obstructed from natural landward movement with increased SLR. Predictions for shoreline retreat, like the Bruun Rule, are controversial and often overly simplified [36]. Modeling shoreline retreat using a Bayesian network has been fruitful in prior studies [37]. Along with shoreline retreat, other factors will likely play a role in shaping these beaches in the future, such as the effects of long-shore drift and the corresponding reallocation of sediments across nesting beaches, wave heights, the potential net loss of offshore sediment, offshore substrate structure, ocean currents, and increased deposition of sediment materials onto current beach habitat during high tidal inundation events [21]. Complex coastal dynamic processes can be expected to alter the morphology of these beaches with some level of shoreline retreat, but these intricate processes have yet to be studied on Bioko and thus render more complex SLR predictive methods incompatible at this time. The ability of surrounding coral reef growth to correlate with increasing sea levels will likely play a key role in the level of sand accretion seen in the upcoming century [21]. IPCC RCP SLR scenarios for the mid to late 21st century are relative to the reference period of 1986–2005, meaning that the results displayed here could be an estimate applicable for at least 11 years after the official year ranges for reported projections [4]. Inconsistencies in total beach area can be attributed to rounding of proportions and slight changes in model resolution. These predictions can be viewed as the best available insight into the future effects of SLR on Bioko's five nesting beaches.

The presence of beach sections on Beaches A and B where nesting habitat between the high tide line and vegetation line has already been completely lost is evidence that even though shoreline retreat will occur over time, the rate of beach erosion is currently faster than the rate of shoreline retreat. Unsurmountable vegetation berms have been left as verification of the discrepancy between beach erosion processes and shoreline retreat. There are no anthropogenic barriers to the landward movement of Bioko's beaches, but rock walls (Beach A) and rivers (Beaches C and D) could be natural barriers [1, 2]. It is likely that a section of Beach A at least 650 m in length will eventually disappear altogether with no inland retreat due to a large rock face directly adjacent to the beach. The face is located farther and farther inland as one moves Southeast along the beach, is at least 50 m tall, and can already be considered the "vegetation line" in some areas.

Previous studies in the Caribbean and Australia conducting similar analyses have reported percent nesting habitat losses that are less than what is reported in this paper [1–3]. This can likely be attributed in part to the higher reported elevation relative to the high tide line of other studied beaches [3]. Fuentes et al. 2010 reported an intuitive decreasing trend between maximum beach elevation and percentage of predicted inundated area. Although this decreasing trend between increasing beach elevation and nesting habitat loss was also observed in the presented dataset, it was not significant. This insignificance can likely be attributed to the fact that the beaches did not have significantly different elevations. Other morphological factors such as beach width and slope did significantly influence habitat loss.

With increasing SLR, increases in the amount of erosion and flooded nests are expected [10] and have been observed already on Bioko [35]. If rains increase in the West African region with climate change, as is suggested with low to medium confidence [38], these beaches are particularly susceptible to increased inundation risk due to rising water tables from both landward and seaward sides. Specific predictions include an increase in the quantity of days experiencing extreme rainfall in West Africa and increased frequency and intensity of rainfall events in the Guinea Highlands and Cameroon Mountains [39–42]. Bioko Island, one of the wettest places in Africa [43], is made up of a complex network of rivers, waterfalls, and lagoons that intersect the beaches at countless points along the shoreline. The fate of one inundated leatherback nest on Beach D is attributable to the high-water table, resulting from a waterfall located directly behind this particular portion of the beach [35].

Creating a hatchery could be an important conservation measure undertaken to protect nests that are likely to be saturated by the tides or rising water tables. Hatcheries have increased the hatching success of sea turtle species on beaches where various anthropogenic and natural threats have made successful in-situ incubation unlikely [44–47]. Although translocating nests can negatively affect embryo development [48, 49], the relocation of otherwise doomed eggs to a hatchery can result in a net gain in hatchlings produced over time [50].

Increased nest inundation will likely cause decreases in the reproductive output of sea turtles [13]. Preliminary predictions that can be made about species-specific vulnerability with increasing SLR are imperative in understanding which species are at greater impending risks with continued climate change. The data suggest that Beach D will be the beach to maintain the largest amount of nesting habitat for the longest period of time, making it theoretically the most vital beach to protect on the entire island. Unfortunately, it is also the beach that is most threatened by the road built in 2014 and corresponding increase in construction planning, tourists, and illegal egg and adult turtle take [8]. Recommendations have been made to the government of Equatorial Guinea to protect Bioko's nesting beaches, and especially Beach D, by minimizing development in the Grand Caldera and Southern Highlands Scientific Reserve and the southern beaches, investing in increased tourist environmental awareness campaigns, and increasing enforcement of existing regulations. With minimal development, natural shoreline retreat will have a chance to preserve intricate beach zoning as the sea level rises. By reporting our findings that the beach that is the least vulnerable to future increases in sea level is also the most vulnerable to anthropogenic encroachment, Beach D, the government of Equatorial Guinea can make more informed decisions about the protection of their endangered wildlife.

Similar studies that deploy this basic modelling technique can be useful globally in identifying priority areas for conservation of sea turtle nesting habitat. In areas where compromises need to be made between conservation and coastal development, basic sea level rise modelling can help authorities know which beaches or areas will be the most viable for sea turtles for the longest period of time. These areas can be prioritized for preservation. This type of site-specific modelling can also be helpful in determining the best areas to focus mitigation efforts, such as the placement of a hatchery, to decrease threats related to sea level rise and beach erosion.

Basic adaptive capabilities of sea turtles to change their behavior and choose locations further up the beach is supported in this study by the statistic that 89% (n = 26) of the time when a leatherback was found digging her nest below the HTL and the nest filled with water, she aborted that nest to choose a drier location closer to the vegetation. As turtle species can shift their nesting grounds when faced with unsuitable nesting habitats [17–20], it is possible that turtles could begin to nest on Beach D more frequently, as the other surrounding beaches experience more nesting habitat loss. This possibility highlights the importance of protecting Beach D from future development. As Bioko hosts the second largest nesting aggregations of leatherback and green turtles in West Africa [8], the reproductive output of these beach habitats is vitally important to the health of the nesting stocks. Losing this nesting habitat to sea level rise would either remove or displace hundreds of individuals of each species [8]. Internesting satellite tracking and genetic studies in the Gulf of Guinea could provide more insight into the nest site fidelity of Bioko's nesting turtles and their potential adaptability to other nesting grounds.

To our knowledge this is the first study to predict the impacts of SLR on sea turtle nesting habitat in Africa and one of the first for a critically important leatherback nesting aggregation worldwide. In the future, advances in modeling methods and increased knowledge of complex coastal processes could be used to improve presented estimates of SLR. These present findings provide a baseline for continued coastal change and habitat use modeling. This study will call attention to the fragility of sea turtle nesting habitat globally and the findings will be valuable to the government of Equatorial Guinea in future developmental planning.

Supporting information

S1 Dataset. Nesting beach profiles.
(XLSX)

S1 Fig. Triangulated irregular network model example. A screenshot of the triangulated irregular network model for Beach D. Displayed are the projected increases in sea level predicted for 2046–2065 scenarios of 0.24, 0.25, 0.26, and 0.3 m and the 2081–2100 scenarios of 0.47, 0.48, 0.63, and 0.75 m.
(PNG)

S2 Fig. Nesting beach satellite and ground images. This figure illustrates the visible space in between the HTL and vegetation line, the current nesting habitat, on Beaches D, C and B. HTL shown in blue and vegetation line shown in green.
(PNG)

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The impacts of extreme El Niño events on sea turtle nesting populations

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Abstract
The El Niño Southern Oscillation (ENSO) is the predominant interannual pattern of climate variability in the world and may become extreme approximately once every 20 years. Climate-forced interannual variability in fecundity rates of long-lived species are well-studied, but the effect of extreme events is less clear. Here, we analyzed the effect of the extreme 2015–16 El Niño event on three long-lived sea turtle species in a region highly influenced by ENSO. The effect of this extreme event varied considerably among species. While reproductive success dramatically declined in leatherback turtles (*Dermochelys coriacea*), the reduction was only marginal in green turtles (*Chelonia mydas*). Nevertheless, the number of nesting green turtles decreased following the extreme El Niño event, likely due to decreased ocean productivity. We used global climate models to project an increase in the decadal occurrence of extreme events from ~ 0.7 events (beginning of twentieth century) to ~ 2.9 events per decade (end of twenty-first century). This resulted in a projected decline in the reproductive success of leatherback turtles (~ 19%), a milder decline in olive ridley turtles (*Lepidochelys olivacea*) (~ 7%), and no decline in green turtles (~ 1%). Extreme El Niño events can have a strong detrimental effect on East Pacific leatherback turtles, a population that is already critically endangered due to other anthropogenic impacts. Our results highlight the importance of conducting species-specific and site-specific analyses of climatic impacts on sea turtles.

Keywords ENSO · Extreme events · Long-lived · Sea turtles · Reproductive success · Climate change

1 Introduction

Global and regional impacts driven by El Niño Southern Oscillation include changes in air temperatures, trade winds, storm activity, and precipitation patterns that can affect wildlife,

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Extended author information available on the last page of the article ecological processes, and local economies (Stenseth et al. 2002; Wolter and Timlin 2011; Cai et al. 2015; Philander 1983). It results from the interactions between the atmosphere and the ocean and is characterized by relative unpredictability (Rasmusson and Wallace 1983), alternating from an El Niño phase, characterized by increased ocean temperature and decreased ocean productivity throughout the eastern Pacific Ocean, and a La Niña phase, when the contrary is true (Chavez et al. 1999).

The natural variability of El Niño Southern Oscillation (ENSO) can occasionally lead to extreme events, such as those occurring in 1982–1983 and 1997–1998. Extreme El Niño events have the potential to cause droughts, fires and floods, damaging ecosystems, agriculture, and fisheries (Cai et al. 2014, 2015; Santoso et al. 2017). For instance, the extreme El Niño event of 1997–1998, considered “the climatic event of the century,” cost billions of US dollars in damage (Cai et al. 2014). Because of its devastating effects on the economy and nature, the relationship between extreme El Niño events and greenhouse gas emissions has received considerable attention in recent years (Cai et al. 2014; Wang et al. 2017). One particular study determined that the frequency of extreme events would increase along with global mean temperatures and double if temperatures rose to the target of 1.5 °C above pre-industrial levels that was set at the Paris Agreement (Wang et al. 2017), which is still considered a moderate climate change scenario (IPCC 2013).

The first extreme El Niño event of the twenty-first century occurred in 2015–16 and its effects were felt worldwide. Extreme droughts and fires were recorded in the northern Brazilian Amazon (Fonseca et al. 2017), substantial beach erosion effected the Northwest coast of the US (Barnard et al. 2017) and floods occurred in Peru (Santoso et al. 2017). The severity of the 2015–16 event was also exacerbated by the unusually warm conditions registered during 2014 (Santoso et al. 2017). The North Pacific region of Costa Rica suffered a severe drought during this time as rainfall there is associated with ENSO (Waylen et al. 1996). North Pacific Costa Rica has a distinctive climate from the rest of the country that is characterized by a rainy season from June to October (with September and October as the rainiest months), followed by a dramatic dry season between December and April (being May and November as transition months). Dry conditions are aggravated during El Niño years causing severe droughts (Waylen et al. 1996) and damaging the local economy, which is largely based on cattle production and therefore, dependent on precipitation levels (Retana and Rosales 2000).

Climate-forced inter-annual variability in fecundity rates is common among long-lived species (Gaillard et al. 1998), but the effect of extreme events has been less studied. Based on number of nesting females, Costa Rica is among the most important regions for sea turtles in the Americas, and it holds nesting populations for all but two of the seven sea turtle species found worldwide. Four species nest in the North Pacific region and three of them, leatherback turtles (*Dermochelys coriacea*), green turtles (*Chelonia mydas*), and olive ridley turtles (*Lepidochelys olivacea*), have significant rookeries, among the most important in the region. In the case of the leatherback turtle, which is critically endangered in the eastern Pacific (Wallace et al. 2013), it has been previously determined to be affected by ENSO. Their fecundity is reduced during dry and warm El Niño years by means of decreased reproductive frequency (Saba et al. 2007) and hatching success (Santidrián Tomillo et al. 2012). Because of the effect of local climate on hatching success, population declines will likely follow under continued climate change (Saba et al. 2012). The effect of ENSO on the other sea turtle populations that use this same region, as well as the potential impact of extreme events on all of them, remain unknown. However, similar impacts could be expected because egg clutches of different species incubate on the same beaches and they all forage in regions of ENSO influence. Leatherback turtles mainly forage on gelatinous zooplankton such as jellyfish in the tropical Pacific (Saba et al. 2008), green turtles on seagrass and algae in coastal areas (Seminoff et al. 2002) and olive ridley turtles are omnivorous, eating a wide range of prey such as crabs, salps, algae, or fish, and can have wide dispersions (Plotkin et al. 1995; Spotila 2004). Given that the eastern tropical Pacific is an area of high influence by ENSO, where the three species are found, we would expect that population declines under increasing frequencies of extreme events, even if other anthropogenic impacts were reverted. The objective of this study was to assess the effect of extreme El Niño events on three different species of sea turtles that nest in Northwest Costa Rica, an area highly influenced by ENSO.

2 Methods

The beaches with the highest abundance of nesting turtles in Pacific Costa Rica are located in the Nicoya Peninsula, Northwest Costa Rica. We obtained information on nesting abundance and reproductive success for three sea turtle species, leatherback (*Dc*), green (*Cm*), and olive ridley turtles (*Lo*) that nest in this area (Table 1). From North to South, these beaches were (species that nest on each beach in brackets) San José Island (*Cm*), Nancite (*Cm, Lo*), Cabuyal (*Cm, Lo*), Playa Grande (*Dc, Lo*), Punta Pargos (*Cm*), and Ostional (*Lo*). Olive ridley *arribadas* occur at Nancite and Ostional. *Arribadas* are synchronic mass nesting events that last a few nights, take place approximately once per month and only happen in a few places worldwide (Fonseca et al. 2009; Valverde et al. 2012). The rest of beaches hosted solitary nesters. For each species, we included nesting beaches that were either considered index (main beaches) or secondary sites depending on the number of nesting turtles and their regional relevance (Santidrián Tomillo et al. 2017a). Thus, a beach could be classified as index beach for a species and secondary for another. Index sites (species in brackets) included San José Island (*Cm*), Cabuyal (*Cm*), Nancite (*Lo*), Ostional (*Lo*), and Playa Grande (*Dc*). Secondary beaches included Nancite (*Cm*), Punta Pargos (*Cm*), Cabuyal (*Lo*), and Playa Grande (*Lo*) (Table 1). Playa Grande (together with the two other smaller beaches that comprise Las Baulas National Park) is the only index site for leatherback turtles in Costa Rica. Because the number

Table 1 Nesting beaches by species, type of beach, and proxy of nesting abundance. All beaches were located in North Pacific Costa Rica and were important nesting sites for the three species that are regular nesters in this area. Type of nesting beach was either index or secondary beach. Proxy for nesting abundance was nests, body pits, and/or females. *nesting beaches where *arribadas* occur

Beach	Species	Beach type	Proxy nesting abundance
Nancite*	*L. olivacea*	Index	Nests
Cabuyal	*L. olivacea*	Secondary	Body pits
Playa Grande	*L. olivacea*	Secondary	Body pits
Ostional*	*L. olivacea*	Index	Nests
Isla San José	*C. mydas*	Index	Nests
Nancite	*C. mydas*	Secondary	Nests
Cabuyal	*C. mydas*	Index	Nests, females
Punta Pargos	*C. mydas*	Secondary	Nests
Playa Grande	*D. coriacea*	Index	Body pits, females

of leatherback turtles at secondary beaches is now very low (~ 3–5 females per year, Santidrián Tomillo et al. 2017a), we did not include any other beach for this species.

2.1 Nesting abundance

Depending on the methodology followed by each monitoring project on each of the study beaches, we used either the number of body pits, nesting females, and/or nests as indicators of nesting abundance, choosing the most reliable estimation in each case (Table 1). We used nesting females as proxy of nesting abundance when beach effort was high and thus all females were likely seen in a season (as they nest multiple times, the probability of missing a turtle every time she nests in a given nesting season is very low when beach coverage is high). Alternatively, when efforts were more directed towards verifying all egg laying than identifying individual females, we used the number of nests. Finally, we used body pits when both the number of females and nests was likely underestimated (i.e., olive ridley turtles at Playa Grande are likely to be missed for the season if they are missed just one time, as most turtles lay only one clutch per nesting season). In this case, all body pits were counted but not necessarily all turtles and nests, as some females were not seen and/or not all egg laying events were verified. The number of nests registered at the *arribadas* at Ostional and Nancite was estimated using the methodology of transects (Gates et al. 1996). We calculated the annual number of females, nests, and/or body pits at each site between October and February (months of the nesting season) for green, leatherback, and solitary olive ridley nesting beaches. Olive ridley solitary nesters also tend to nest outside of that time frame, but the core of nesting activity still coincides with that of the other species. Nevertheless, the nesting period at the *arribada* beaches is slightly different as these events may occur year-round. For Ostional, we included data on nesting abundance between July of 1 year to June of the next and for Nancite, between July of 1 year to February of the next (since there are no *arribadas* there between March and June). Because the proxy used to measure nesting abundance varied between sites, we compared nesting trends but not numbers between locations.

We used the multivariate ENSO index (MEI) as an indicator of the strength of El Niño events and compared it to nesting abundance. We used mean MEI values for the same year (January–December) of the nesting season ($\mathrm{MEI}_{\mathrm{current}}$), for the year before (MEI-1), for 2 years before (MEI-2), and for 3 years before (MEI-3), because sea turtles normally migrate to the nesting beach every 2–4 years (Saba et al. 2007). The MEI data were available at https://www.esrl.noaa.gov/psd/enso/mei/.

2.2 Reproductive success

We used hatching success (percentage of eggs that hatch in a clutch) as an indicator of reproductive success and estimated it following the formula $H = S/(S + U)$, where S corresponded to the number of eggshells left by hatchlings that hatched successfully from the egg and U corresponded to the number of unhatched eggs. Eggshells were only counted as one egg when at least 50% of the shell remained (Miller 1999). We estimated annual hatching success for each species at each beach using the mean value for all clutches laid over a nesting season as defined above. We included data from clutches laid between July and February for both *arribada* nesting beaches. Although *arribadas* in Ostional can occur throughout the year, these are typically very small during the dry season and with no hatchling production due to hot and dry conditions. Therefore, data was not available from February onward. In addition, we did not use hatching success data for the green turtles of Nancite and Punta Pargos, as the sample size was too low in Nancite (not determined for 2 years) and all clutches were relocated at Punta Pargos due to a high risk of being poached and therefore, did not incubate in natural conditions. To compare hatching success with local climatic conditions, we obtained local climate data (air temperature and precipitation) from a nearby weather station at the Liberia airport (< 70 km from all nesting sites), Northwest Costa Rica, facilitated by the National Meteorological Institute of Costa Rica. We used the MEI values ($\mathrm{MEI_{rainy}}$) that corresponded to the months of the rainy season in Northwest Costa Rica (May through October), as precipitation is influenced by ENSO and it has been shown that it greatly affects hatching success of leatherback turtles in this area (Santidrián Tomillo et al. 2012).

2.3 Projections of the effect of extreme events on reproductive success

We considered that an El Niño event became extreme when the average austral summer rainfall was greater than 5 mm/day as defined in previous studies (Cai et al. 2014). We used historical output (years 1850–2005) and the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway RCP8.5 projections from 6 global climate models (CanEMS2, CESM_CAM5, CNRM-CM5, GFDL_CM3, GISS-E2-H, and MRI_CGCM3) that resolve present-day ENSO dynamics and feedbacks (Wang et al. 2017) from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The datasets were accessed from the Earth System Grid Federation (ESGF) at https://esgf-node.llnl.gov/projects/esgf-llnl/. We determined the occurrence of extreme events for each model between 1850 and 2100 and calculated the average number of events over particular time periods to detect changes in frequency.

To assess how the frequency of extreme events affects the reproductive success of the turtles, we calculated reproductive success as the mean annual production of hatchlings over a decade considering the frequency of extreme events projected by the global climate models for that time frame. Then, we compared the mean reproductive success of turtles nesting on the second half of the nineteenth century and first and second half of the twentieth and twenty-first centuries. The annual production of hatchlings was estimated for each species using the following formula:

$$\mathrm{AH} = \mathrm{ECF} \times \mathrm{cs} \times \left(\mathrm{f_1(H_1)} + \mathrm{f_2(H_2)}\right)$$

where AH was the mean annual production of hatchlings, *ECF* corresponded to the mean estimated clutch frequency (number of clutches laid in a season) for the nesting population (estimated as the mean ECF of all turtles for which it has been estimated), *cs* to the clutch size (mean number of eggs in a clutch), f_1 and f_2 to the frequencies of extreme and regular ENSO years, respectively, over a decade, and H_1 and H_2 to hatching success under extreme and regular ENSO conditions, respectively. Mean (± SD) clutch size and ECF were obtained from the long-term monitoring project at Playa Grande for leatherback turtles (66 ± 16.6 eggs and 6.1 ± 3.1 clutches, respectively) and from published articles available for the area for green (76.9 ± 18.2 eggs and 4.3 ± 2.3 clutches) (Santidrián Tomillo et al. 2015a) and olive ridley turtles (87.5 ± 33.6 eggs and 2.2 ± 1.1 clutches) (Van Buskirk and Crowder 1994; Dornfeld et al. 2015). Values of *ECF*, *cs*, and H_1 were obtained by randomly picking one value within the standard deviation of their mean to account for natural stochasticity. We ran the model 100,000 times using the function rnorm in R and averaged the resulting values. For H_2, we used the standard deviation corresponding to years with regular ENSO conditions.

2.4 Statistical analyses

We used R version 3.5.0 (R Core Team 2018) and Statistical Package for Social Sciences (SPSS) version 24 (IBM Corp 2016) to conduct statistical analyses. We detrended nesting abundance time series for each beach using the detrended function of the practical numerical math functions (PRACMA) package in R and used Pearson correlations to compare detrended values to the MEI values ($\mathrm{MEI}_{\mathrm{current}}$, MEI-1, MEI-2, and MEI-3). We used the Shapiro-Wilk test to assess for normality in the distributions of nesting abundance. Finally, we tested for possible autocorrelation between years in nesting abundance on the detrended time-series and the actual values using the autocorrelation function (ACF) in R. We used SPSS to run Pearson correlations between MEI and local climatic conditions and linear regressions to test the effect of MEI on hatching success.

3 Results

Local climatic conditions were correlated with the MEI during the months of the rainy season, both with (1) precipitation accumulated ($r = -0.689$, $P < 0.01$, $n = 39$ years) and (2) air temperature (°C) over the same time period ($r = 0.649$, $P < 0.01$, $n = 39$ years). The 2015–16 El Niño event greatly influenced local climatic conditions in northern Costa Rica, being the hottest and driest year since registers started in 1976. This means that despite being of lower intensity than the 1997–98 El Niño extreme event, the influence of the 2015–16 event on local climate was larger, surpassing all previous records (Fig. 1). Additionally, the extremely hot and dry conditions registered in 2014 (Fig. 1) likely exacerbated the impact of the 2015–16 El Niño event in this area.

Although there was some level of autocorrelation among years in the nesting abundance of each species and site, this was not statistically significant for any time-series ($P > 0.05$ all cases). We did not find a general effect of ENSO on nesting abundance in leatherback, green, or olive ridley turtles when comparing MEI values to the detrended nesting values ($P > 0.05$ all cases). Nesting abundance of green turtles was low during the El Niño event (2015–16) and lower during the year after (2016–17), and was followed by an increase in 2017–18 (Fig. 2). The same trend was found in all green turtle nesting beaches and the numbers were highly correlated among beaches ($P < 0.05$ all cases). Nesting abundance of olive ridley turtles appeared unaffected by the 2015–16 event (Fig. 2).

Hatching success was strongly influenced by $\mathrm{MEI}_{\mathrm{rainy}}$ over 6 years in leatherback turtles (linear regression: $R^2 = 0.977$, $P < 0.001$) and olive ridley turtles at Playa Grande (linear regression: $R^2 = 0.809$, $P = 0.01$), but not at any other olive ridley site nor at any of the green turtle nesting beaches ($P > 0.05$, all cases) (Fig. 3). Hatching success of all species and at all locations was lowest in 2015–16 (Fig. 4). The effect was strongest in leatherback turtles that led to nearly no production of hatchlings that year (mean ± SD in 2015–16, 4% ± 12%), while the effect was very mild in green turtles (just 6% lower than their mean) (Fig. 4). Hatching success of leatherback turtles was by far the lowest in the history of the monitoring project at Playa Grande, which began assessing hatchling production in 2004, and almost no hatchlings were produced coinciding with the extreme El Niño event.

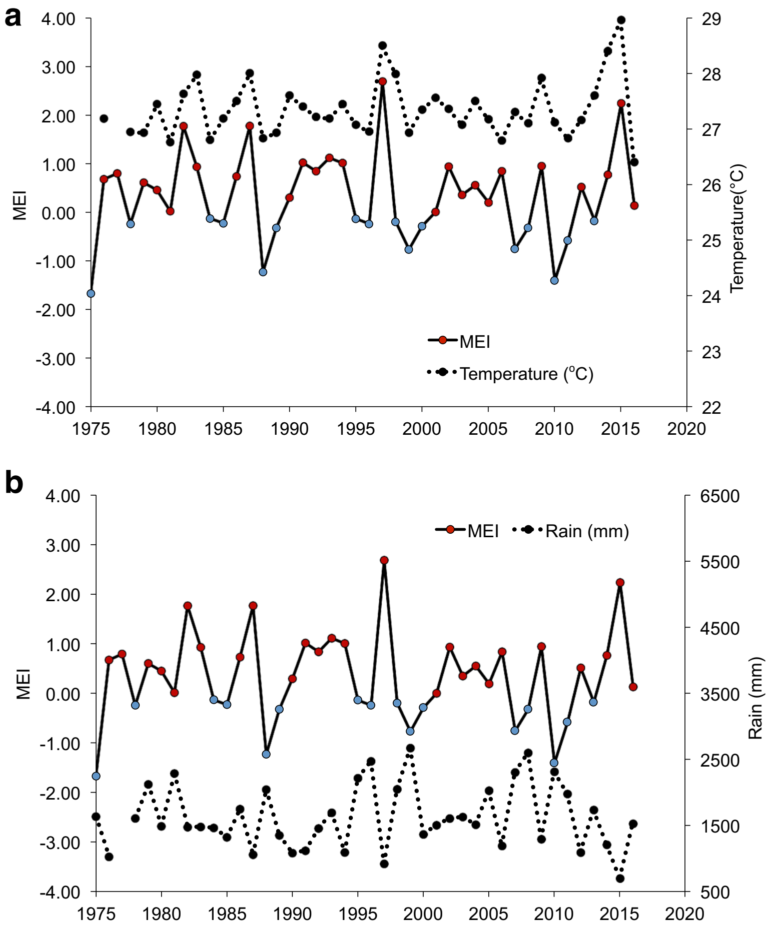

Fig. 1 Average multivariate ENSO index (MEI) and local climatic conditions in North Pacific Costa Rica. Local climatic conditions correspond to **a** local air temperature (°C) and **b** precipitation (mm) registered between 1975 and 2016 during the rainy season (May–November). Red circles indicate El Niño and blue circles La Niña events. MEI values represent averages for the same months of the rainy season

Under the RCP8.5 scenario, climate models projected a four-fold increase in the frequency of extreme events between the end of the nineteenth century and end of twenty-first century (Table 2), from 0.7 events per decade during the second half of the nineteenth century, to 1 event per decade during the second half of twentieth century and to 2.9 events per decade projected by the second half of twenty-first century. This translated into an estimated decline in the mean annual reproductive success over a decade of ~ 19, 1, and 7% in leatherback, green, and olive ridley turtles, respectively (Table 3).

4 Discussion

Climate change has become a growing threat to sea turtle populations as rising temperatures and changes in precipitation patterns can potentially impact foraging dynamics, reduce

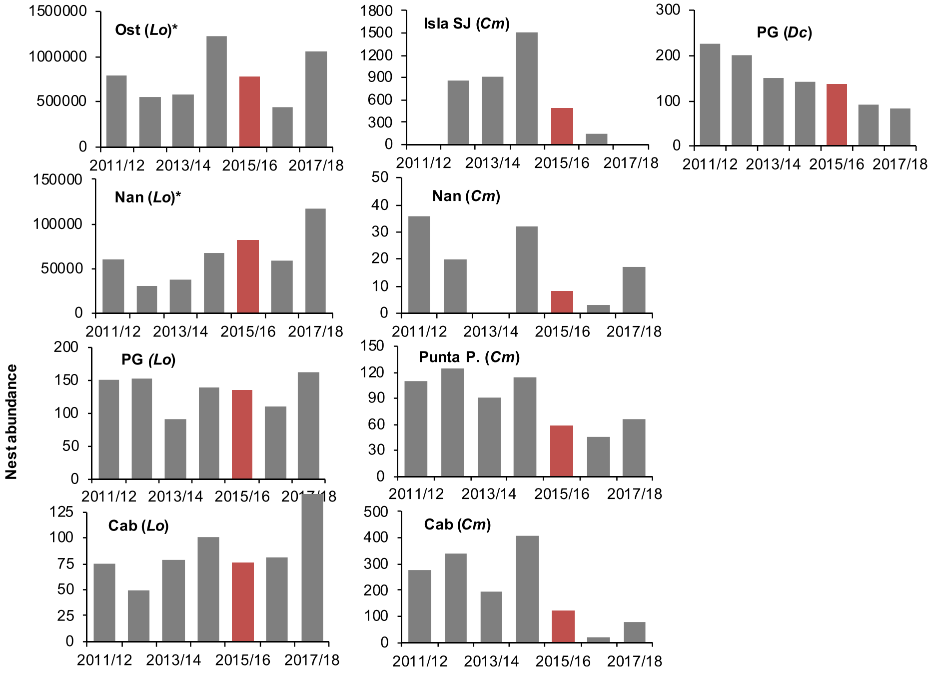

Fig. 2 Nesting abundance of three sea turtle species that nest in North Pacific Costa Rica. Nesting abundance is indicated by number of (1) nests in green turtles (*Cm*) and "*arribada*" olive ridley turtles (*Lo*)* and (2) body pits in leatherback (*Dc*) and solitary olive ridley turtles (*Lo*). Beaches included were (North to South) Isla San José (*Cm*), Nancite (*Cm, Lo*), Cabuyal (*Cm*, *Lo*), Playa Grande (*Dc*, *Lo*), Punta Pargos (*Cm*), and Ostional (*Lo*). * indicates arribada nesting beaches. No data was available for green turtles at Isla San José and Nancite in 2011 and 2013, respectively. Year of the extreme El Niño event is indicated in red

hatchling output, reproductive frequencies, and/or further bias sex ratios of hatchlings. In some areas along the eastern Pacific coast, such as northern Costa Rica, El Niño events drive changes in local climate towards detrimental conditions for sea turtles. Thus, an increase in the frequency and/or strength of these events could have severe impacts on sea turtles. In the present study, we (1) assessed the impact of extreme El Niño events on three sea turtle species that nest in northwest Costa Rica and (2) projected changes in the frequency of extreme events due to climate change to see how this would affect sea turtle populations.

Hatching success of sea turtle eggs was found to be negatively affected by high temperatures in several sea turtle species and populations (Howard et al. 2014; Montero et al. 2019; Santidrián Tomillo et al. 2009; Valverde et al. 2010). In leatherback turtles, high nest temperature and specially, low precipitation levels increase mortality of eggs and hatchlings in the nest, conditions that are exacerbated during regular El Niño years (Santidrián Tomillo et al. 2012). Local climate in northwest Costa Rica reached extreme conditions in 2015, the hottest and driest year since there were records (Fig. 1). Consequently, the extreme El Niño events had a dramatic effect on the hatching success of leatherback turtles with only 4% of eggs hatching in 2015/16.

Hatching success of leatherback turtles in Costa Rica seems more susceptible to changes in the local climate than in other areas around the world such as the Caribbean and South Africa, possibly due to the generally drier conditions that characterize northwest Costa Rica (Santidrián Tomillo et al. 2015b). Local climatic effects on hatching success have also been

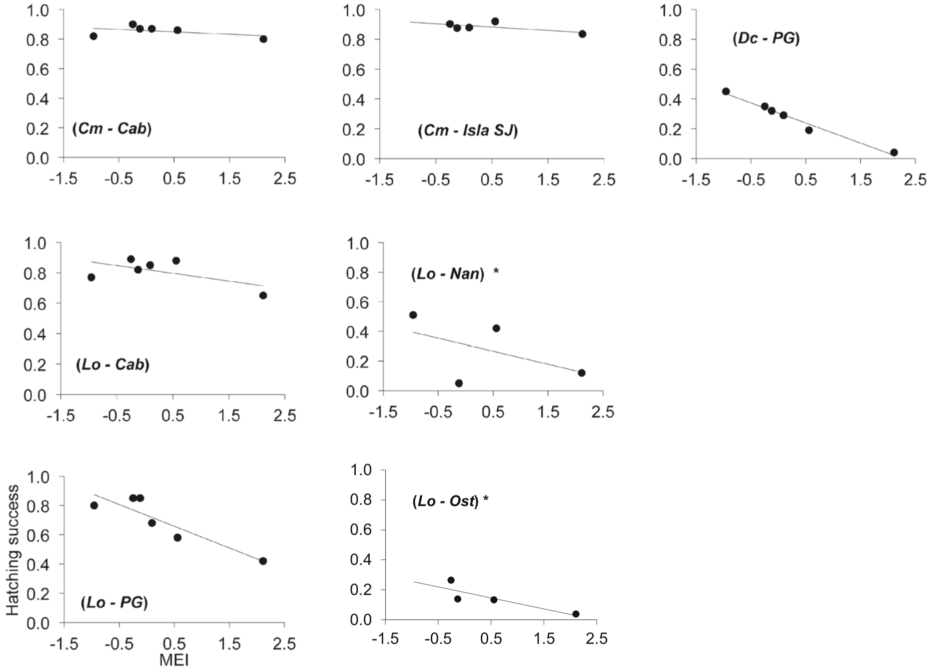

Fig. 3 Annual sea turtle hatching success in Northwest Costa Rica versus the multivariate ENSO index (MEI). Annual hatching success of leatherback (*Dc*), green (*Cm*), and olive ridley (*Lo*) turtle nests between seasons 2011/2012 and 2016/2017 was obtained from Playa Grande (*Lo, Dc*), Nancite (*Lo*), and Cabuyal (*Lo, Cm*). * indicates arribada nesting beach

reported for loggerhead turtles in Brazil where some differences were found among beaches along the coast (Montero et al. 2019). We also found some differences in the hatching success of olive ridley turtles among beaches in Costa Rica. Nevertheless, decreases were observed at most sites due to the extreme event in both solitary beaches (with still ~ 40 and ~ 65% of eggs hatching) and in Ostional. This suggests that olive ridley turtles, while still vulnerable to changes in climate, are less vulnerable than leatherback turtles. Yet the interpretation of the variability in hatching success in *arribada* beaches is complicated as contamination also reduces hatching success due to the extremely high density of nests (Honarvar et al. 2008). Green turtles on the contrary, appeared largely unaffected by ENSO. Hatching success decreased during the extreme event, but it was still high at ~ 80% at both index beaches for this species (Fig. 4). This indicates a possible resilience of green turtle clutches to climate change, at least in this area, an interesting characteristic that demands further research.

Although extreme events can negatively affect sea turtles, they are long-lived organisms and the impact of an extreme event on their populations could be buffered over long time periods as they reproduce multiple times during their life. This may be the case for green and olive ridley turtles for which, we projected no impacts or very mild long-term effects. However, in leatherback turtles in Pacific Costa Rica, where reproductive success is strongly associated with local climatic conditions, an increase in the frequency of extreme events could lead to a 19% decline in their mean decadal reproductive success. This adds additional pressure to an already reduced nesting population of leatherback turtles, which are critically endangered in the eastern Pacific due to interaction with fisheries, past egg poaching, and climate change (Saba et al. 2012; Santidrián Tomillo et al. 2008, 2017b; Spotila et al. 2000).

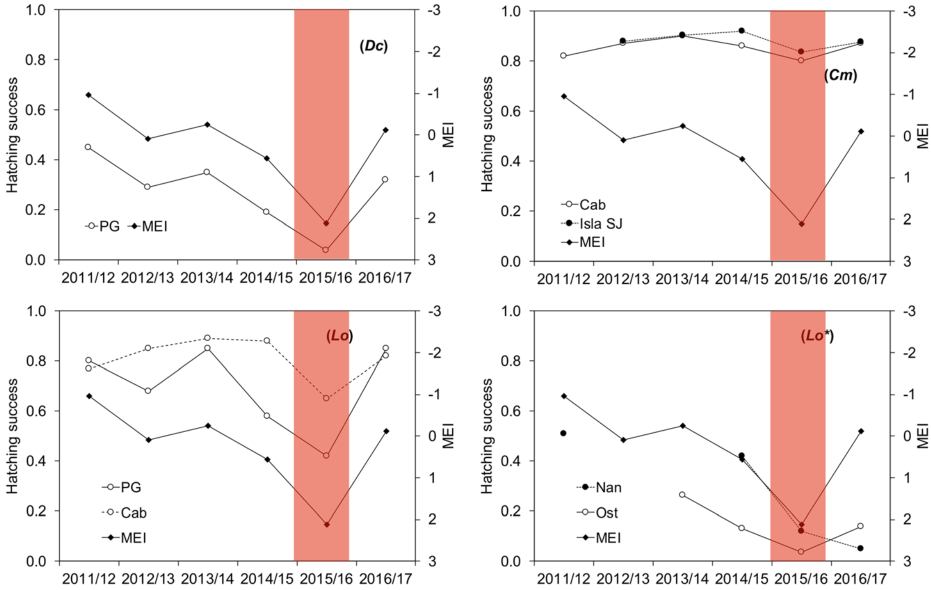

Fig. 4 Changes in annual sea turtle hatching success in Northwest Costa Rica. Annual hatching success of green (*Cm*), olive ridley (*Lo*), and leatherback turtle (*Dc*) nests and the multivariate ENSO index (MEI) between 2011 and 2012 and 2016 and 2017. Beaches included were (North to South) Isla San José (Isla SJ), Nancite (Nan), Cabuyal (Cab), Playa Grande (PG), and Ostional (Ost). The red section indicates the duration of the extreme El Niño event and *indicates the *arribada* nesting beaches. MEI values are in reverse order

Nesting abundance of green turtles was likely affected by the extreme 2015–16 El Niño event. Sea turtles are capital breeders that store energy before migrating and may skip reproduction if foraging conditions are not optimal in a particular year (Saba et al. 2007; Rivalan et al. 2005). Consequently, the number of nesting turtles registered on the beach may be affected by the foraging conditions in the ocean in months or years before the nesting season, as well as by the number of turtles registered in previous seasons (Broderick et al. 2001; Solow et al. 2002). The number of nesting green turtles in northern Australia was related to the ENSO conditions registered 2 years before, with very high numbers occurring after major El Niño

Table 2 Number of extreme events detected by the CMIP5 models. Climate change models included historical (years 1850–2000) and RCP8.5 projections (years 2006–2100). We considered an extreme event when the average austral summer (December–February) rainfall over El Niño 3 was greater than 5 mm per day based on Cai et al. (2014)

	Historical			RCP8.5	
Model	1850–1900	1901–1950	1951–2000	2006–2050	2050–2100
CanESM2	6	6	6	10	17
CESM_CAM5	6	2	9	6	10
CNRM-CM5	1	2	4	4	14
GFDL_CM3	5	3	5	11	14
GISS-E2-H	4	9	5	16	26
MRI_CGCM3	0	0	0	0	6
Mean	3.7	3.7	4.8	7.8	14.5
Mean per decade	0.7	0.7	1	1.7	2.9

events (Limpus and Nicholls 1988). We did not find such an apparent effect of ENSO on the number of green turtles in Costa Rica, with the exception of the 2015/16 El Niño event when nesting abundance was also minimal 1 year after the extreme event. A lack of correlation between MEI and nesting numbers in the whole dataset may be explained by high number of years needed to identify long-term patterns and/or because ENSO conditions occurring in most of the years included in the study were mild (five of the 7 years were on average of neutral conditions; MEI values between − 0.5 and 0.5). It is also possible that the relationship between remigration intervals, oceanic conditions, recruitment rates, and nesting numbers are especially complex in the eastern Pacific due to its lower and variable productivity compared with that of other areas. Thus, more years of data and/or more complex modeling may be needed.

Although the low number of nesting leatherback turtles is also explained by a long-term declining trend due to other impacts (Spotila et al. 2000), the effect of ENSO on their reproductive frequency has been previously determined (Saba et al. 2007), which ultimately, may affect the number of turtles registered on the beach. Likewise, the remigration intervals of green turtles could relate to changes in feeding conditions driven by changes in ocean temperature, affecting the number of nesting turtles on the beach as it occurs in the Caribbean and Australia (Limpus and Nicholls 1988; Solow et al. 2002). Variation in remigration intervals is higher in green turtles than in other sea turtle species, which can largely affect the interannual nesting numbers (Broderick et al. 2001). In addition to the effect on the length of the remigration intervals, which has implications for the short and long-term reproductive success of the turtles, food availability could negatively impact the viability of green turtle populations if adult mortality was increased during years of lower productivity. Long-lived sea turtles are more sensitive to changes in adult mortality than in the mortality of early life stages (Heppell et al. 2003). Thus, an effect of extreme events on adult survival could greatly impact their populations. However, at this moment, we cannot assess the relationship between feeding conditions and adult mortality as long-term datasets would be needed.

The different life histories of closely-related species may also explain some of the differences found on the impacts of extreme events. Nesting abundance of olive ridley turtles appeared unaffected by the 2015–16 El Niño. Unlike the other species, olive ridleys follow a slightly different strategy and only lay 1–2 clutches per year and reproduce every year (Dornfeld et al. 2015). This may allow them to lay clutches “as they become ready” in comparison to the other species that need to store enough energy before migrating to lay multiple clutches in a season and survive that time without feeding (Plot et al. 2013). Interestingly, we also found differences

Table 3 Mean estimated annual number of hatchlings produced per female over a decade. The annual number of hatchlings for leatherback, green, and olive ridley turtles was estimated in relation to the frequency of extreme events projected from the CMIP5 models (0.7, 1, and 2.9 events/decade for second half of the nineteenth, twentieth, and twenty-first centuries, respectively). The percentage decline in hatchling production due to extreme events was estimated based on climate change projections over 100 years (second half of the twentieth century to second half of the twenty-first century)

	Annual number of hatchlings per female			
	1851–1900	1951–2000	2051–2100	% decline due to extreme events
Leatherback turtle	121 ± 81	118 ± 78	96 ± 65	18.6%
Green turtle	290 ± 174	289 ± 174	285 ± 171	1.4%
Olive ridley turtle	151 ± 102	150 ± 101	140 ± 94	6.7%

among olive ridley nesting beaches, which suggest that the impacts of ENSO and extreme events may differ and should be assessed at a very local level.

Finally, differences among beaches and species suggest that some populations could bounce back after extreme events, whereas in others, the effects are more long-term and could even be devastating. As aforementioned, the vulnerability of certain populations to extreme events is likely to be exacerbated if their current population levels are already low and they are threatened by other anthropogenic impacts (Spotila et al. 2000) as is the case in critically endangered eastern Pacific leatherback turtles. Thus, extreme events in this species could lead to rapid extinctions given the large impact that these events have on them and the low nesting levels and the impact of other threats. In addition to the global effect of anthropogenic-forced climate warming, sea turtles in areas highly influenced by ENSO are affected by the periodic occurrence of extreme events. Therefore, sea turtles in this region must adapt if they are to survive throughout the twenty-first century, not only to the increasing global mean temperatures (GMTs), but also to an increasing frequency of extreme events that could double even under small levels of warming (Wang et al. 2017). Some climate mitigation strategies could be implemented to counteract the negative effect of high temperature and dryness on the clutches of species affected, such as nest shading or nest irrigation during extreme El Niño events. Because sea turtles have long-generation times, they may not be able to adapt quick enough to the current rate of change. Thus, a proportion of clutches in risk could be relocated to climate-controlled hatcheries where climate mitigation programs could be conducted. Finally, other extreme events such as prolonged precipitation (Rivas et al. 2018), hurricanes, or harmful algal blooms such as red tides could also impact sea turtles, which have not been considered here. Our results highlight the importance of conducting species-specific and site-specific analyses of climate impacts on sea turtles.

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Author contributions PST, LGF, MW, NT and NJR discussed the implications of the extreme 2015–16 El Niño event in Costa Rica and conceived the study. PST, NJR and FVP led and provided data for the projects at Cabuyal and Playa Grande, LGF led and provided data for the projects at Nancite and Isla San José, MW and NT led and provided data for Punta Pargos and CMO led and provided data for Ostional. VSS advised and assisted with the projections of extreme events. PST wrote the manuscript with input from all authors.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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