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FORECASTING THE VIABILITY OF SEA TURTLE EGGS IN A WARMING WORLD

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Abstract

Animals living in tropical regions may be at increased risk from climate change because current temperatures at these locations already approach critical physiological thresholds. Relatively small temperature increases could cause animals to exceed these thresholds more often, resulting in substantial fitness costs or even death. Oviparous species could be especially vulnerable because the maximum thermal tolerances of incubating embryos is often lower than adult counterparts, and in many species mothers abandon the eggs after oviposition, rendering them immobile and thus unable to avoid extreme temperatures. As a consequence, the effects of climate change might become evident earlier and be more devastating for hatchling production in the tropics. Loggerhead sea turtles (*Caretta caretta*) have the widest nesting range of any living reptile, spanning temperate to tropical latitudes in both hemispheres. Currently, loggerhead sea turtle populations in the tropics produce nearly 30% fewer hatchlings per nest than temperate populations. Strong correlations between empirical hatching success and habitat quality allowed global predictions of the spatiotemporal impacts of climate change on this fitness trait. Under climate change, many sea turtle populations nesting in tropical environments are predicted to experience severe reductions in hatchling production, whereas hatching success in many temperate populations could remain unchanged or even increase with rising temperatures. Some populations could show very complex responses to climate change, with higher relative hatchling production as temperatures begin to increase, followed by declines as critical physiological thresholds are exceeded more frequently. Predicting when, where, and how climate change could impact the reproductive output of local populations is crucial for anticipating how a warming world will influence population size, growth, and stability.

Introduction

Ambient temperatures are warmer in many tropical regions than elsewhere, which allows a wide range of ectotherms to use the external environment to maintain body temperatures near their physiological optimum (Deutsch *et al.* 2008; Huey *et al.* 2009; Kearney *et al.* 2009; Sinervo *et al.* 2010; Sunday *et al.* 2011; Tewksbury *et al.* 2008). As a consequence, the maximum temperature that individual species can withstand has coevolved with preferred body temperature; generally, tropical species live closer to their physiological optimum than closely-related temperate species (Deutsch *et al.* 2008; Grigg & Buckley 2013; Sunday *et al.* 2011). Exceeding this optimum, however, can be costly and dangerous. The safety margin between the optimal temperature range and lethal maximum is often quite narrow (Huey *et al.* 2009; Tewksbury *et al.* 2008; Vickers *et al.* 2011), and climate change could make it more difficult for some tropical species to avoid overheating (Deutsch *et al.* 2008; Kearney *et al.* 2009; Logan *et al.* 2013; Sinervo *et al.* 2010; Tewksbury *et al.* 2008). In temperate environments, many species are living below their optimal temperatures much of the time, and increases in temperature are predicted to benefit a wide range of physiological processes (Deutsch *et al.* 2008; Hays *et al.* 2010; Katselidis *et al.* 2012; Kearney *et al.* 2009; Sinervo *et al.* 2010). This may also be the case for some tropical species, depending on interactions among habitat use, preferred body temperature, and critical thermal maximum (Logan *et al.* 2013; Storch *et al.* 2005). Through the same mechanism, species distributed across a wide range of different climatic conditions (e.g., latitude, altitude, canopy cover, water depth) may be able to adaptively respond to climate change, depending on how temperature increases interact with important physiological thresholds at local spatial scales (Fossette *et al.* 2012; Witt *et al.* 2010). These patterns make understanding when, where, and how local populations will experience the effects of climate change a difficult task, especially for widespread species.

Mobile organisms may be able to ameliorate some of the impacts of warming by changing activity patterns (Fossette *et al.* 2012; Huey *et al.* 2009; Kearney *et al.* 2009; Schofield *et al.* 2009; Sinervo *et al.* 2010), habitat use (Kearney *et al.* 2009; Logan *et al.* 2013), or dispersing to limit thermal stress (Pike 2013b; Witt *et al.* 2010). For example, many large marine species select for temperature at spatial scales spanning microhabitats to regions, which can influence seasonal and daily movements and activity patterns (Rasmussen *et al.* 2007; Schofield *et al.* 2009). The opportunity to avoid stressful thermal conditions may be much more restricted during life stages when mobility is limited (Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Mitchell *et al.* 2008; Telemeco *et al.* 2013; Telemeco *et al.* 2009). If the thermal environment becomes unfavourable, organisms with limited mobility may be unable to avoid stressful temperatures (e.g., by shade seeking, altering activity times, etc.) and thus may be at increased risk of physiological stress and possibly death. In fact, the physical locations of immobile life stages may depend upon external factors, such as nest-site placement by the mother (Hays *et al.* 1995; Wood & Bjorndal 2000) and local environmental conditions (Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Pike 2013a). Females of many species select nest sites based on temperature, because of its direct effects on embryonic development, incubation duration, hatchling body size, and offspring survival (Ackerman 1997; Davenport 1997; Telemeco *et al.* 2013; Telemeco *et al.* 2009). In some cases, however, climate change could alter the landscape such that the microhabitat characteristics formerly selected by females become rare or unavailable (Katselidis *et al.* 2012; Mitchell *et al.* 2008; Telemeco *et al.* 2013; Telemeco *et al.* 2009; Witt *et al.* 2010). This could lead to widespread changes in nest temperatures, which could directly alter hatchling phenotypes (including sex for species with temperature-dependent sex determination; Fuentes & Porter 2013; Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Telemeco *et al.* 2009, 2013) or increase embryonic mortality (Tapilatu & Tiwari 2007).

Research into the direct effects of climate change on the vulnerable egg stage of terrestrial animals has focused on the sex ratios of the offspring in species with temperature-dependent sex determination. Primary sex ratios can directly influence population growth rates, and chronically-biased sex ratios could lead to population bottlenecks or even population collapse (Hays *et al.* 2003; Katselidis *et al.* 2012; Witt *et al.* 2010). To date, however, a much more important aspect has been overlooked: survival of the embryos. If temperatures inside the nest exceed the point at which embryonic survival decreases substantially, this could be magnify any potential demographic consequences associated with skewed sex ratios or other sublethal temperature effects. Large-scale egg mortality due to overheating already has been observed on some tropical sea turtle nesting beaches (Tapilatu & Tiwari 2007), and widespread changes in hatchling phenotypes have been predicted for a range of reptiles (Fuentes & Porter 2013; Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Katselidis *et al.* 2012; Mitchell *et al.* 2008; Telemeco *et al.* 2009, 2013; Witt *et al.*, 2010). To date, however, we have almost no understanding of how climate change could influence offspring production, mediated through hatching success of the eggs, across the entire distribution of widespread species. Thus, our understanding of how climate change could influence life history and population demography of ectotherms is limited.

Loggerhead sea turtles (*Caretta caretta*) have the widest nesting range of any living reptile, spanning temperate to tropical latitudes in both hemispheres (Pike 2013a). Loggerhead sea turtles generally nest sympatrically with the other six species of sea turtle, but are distributed further north and south. Sea turtle nesting beaches are at risk from sea level rise, which could reduce the amount of nesting habitat available and increase the water table, both of which could reduce habitat quality and reproduction (Fish *et al.* 2005, 2008; Fuentes *et al.* 2011). The embryos of all sea turtle species show similar functional responses to temperature (i.e., fixed upper lethal temperatures of 35°C; Ackerman 1997; Davenport 1997;

Witt *et al.* 2010), which led me to predict that the local effects of climate change on hatching success would be most pronounced in tropical regions. To understand how climate change could impact loggerhead sea turtle reproduction, I predicted spatial and temporal patterns of egg hatching success across the geographic range of this widespread species.

Materials and Methods

Modeling approach.— I used MaxEnt version 3.3.3k (Phillips *et al.* 2006; Phillips & Dudík 2008) to model loggerhead sea turtle nesting distributions under current and predicted future climate scenarios. This approach combines environmental variables with known nesting locations and randomly-selected background locations to predict the potential distribution of nesting using the principle of maximum entropy (Phillips *et al.* 2006; Phillips & Dudík 2008). Model input consisted of 933 georeferenced nesting beach locations for loggerhead turtles (compiled from State of the World's Sea Turtles and the Wider Caribbean Sea Turtle Conservation Network; Dow Piniak & Eckert 2011; Pike 2013a) and nine climate variables (mean daily range in temperature, isothermality, maximum temperature of the warmest month, annual temperature range, precipitation seasonality, and precipitation of the wettest, driest, warmest, and coldest quarters; Hijmans *et al.* 2005). These climate variables encompass broad annual and seasonal patterns of temperature and rainfall globally (Pike 2013a), and thus are relevant to loggerhead sea turtle nesting, which shows strong geographical variation in seasonality (reviewed by Dewald & Pike 2013). Climate variables covered land areas at a resolution of 4km x 4km, which was restricted to within ~8km (two grid cells) of the ocean to improve model performance (Pike 2013a, 2013b).

MaxEnt uses these climatic predictor variables to quantify the probability of sea turtle nesting occurring in each grid cell, ranging from 0 to 1, with values near 0.5 representative of average habitat quality (Phillips & Dudík 2008). The climatic predictor variables were used to discriminate nesting and non-nesting locations using threshold relationships. I used 10-fold crossvalidation to randomly partition the full set of nesting locations into 10 approximately equal datasets. During each of 10 model runs, nine of the data partitions are used to train the model and these results are tested against the tenth partition (for full details on the process of model building, testing, and selection see Pike 2013a, 2013b). For all analyses I used the median habitat suitability value across all 10 runs of the model.

I calibrated distribution models using current climatic conditions (averaged over ~1950-2000; for full details on climate data, see Hijmans *et al.* 2005), and projected the final model onto future predicted climate surfaces. I used four climate change models (Canadian Centre for Climate Modelling and Analysis, Commonwealth Scientific and Industrial Research Organisation, Hadley Centre for Climate Prediction and Research (UK), and National Institute for Environmental Studies) under three emission families (A1, A2A, B2A) that encompass the central 80% of climate change predictions for 2020, 2050, and 2080 (total of 36 future scenarios; Intergovernmental Panel on Climate Change 2007; Special Report on Emission Scenarios, 2000). These estimates encompass current rates of temperature increase (i.e., a 2-7°C increase by 2100; Special Report on Emission Scenarios, 2000), and thus are a good approximation of the range of conditions likely to be experienced in the coming decades. The A2A family predicts a temperature increase within the range of 2.0-5.4°C, relative to 1980-1999 (best estimate = 3.4°C; Special Report on Emission Scenarios, 2000). The B2A family predicts a temperature increase within the range of 1.4-3.8°C (best estimate = 2.4°C; Special Report on Emission Scenarios, 2000). The A1 family is intermediate to these high and low predictions.

I explored how climate change could influence the maximum temperature of the warmest quarter (i.e., summer, during which many loggerhead sea turtle populations are nesting; Dewald & Pike 2013) at two spatial scales: (1) regional (temperate vs tropical latitudes) and (2) among spatially and biologically distinct populations that differ in conservation status and threats (Regional Management Units, defined and delimited by Wallace *et al.*, 2010). Loggerhead turtles encompass eight Regional Management Units, two of which span both temperate and tropical latitudes. For each loggerhead nesting beach I extracted temperature data from the spatial climate datasets. These temperatures and predicted hatching success (see below) were compared among regions and Regional Management Units under different climate scenarios.

Empirical hatching success.— I used published loggerhead hatching success data from undeveloped nesting beaches (n = 21), expressed as the mean proportion of eggs hatching from each clutch (Pike 2008, 2009). These beaches were categorized as temperate or tropical based on latitude (tropical locations range between 23°26′16″N and 23°26′16″S), and habitat quality was estimated using the MaxEnt habitat suitability score for current climatic conditions. These hatching success data were obtained from different studies conducted in different years and averaged over varying time intervals, but are the best currently available (Pike 2008, 2009). To test for differences in egg viability between temperate and tropical beaches, I used ANOVA with nesting beach location (temperate or tropical) as the factor and hatching success as the dependent variable. I used logarithmic regression to test for an empirical relationship between habitat suitability and hatching success.

Forecasting hatching success.— Species distribution modeling is a powerful way to derive a single measure of local habitat quality (i.e., suitability, probability of occurrence) across the geographic range of a species from complex environmental datasets (Phillips & Dudík 2008). These measures of habitat quality can be linked to population-level ecological traits, such as genetic diversity (Dubey *et al.* 2013), abundance (Kulhanek *et al.* 2011), maximum population size (VanDerWal *et al.* 2009), or offspring production (Brambilla & Ficetola 2012), and predicted across the landscape under current and future climate scenarios (Dubey *et al.* 2013). I created spatial and temporal predictions of hatching success using the regression equation relating habitat suitability to hatching success. I extracted hatching success estimates for loggerhead nesting beaches, and graphed predicted hatching success at known tropical and temperate nesting beaches under current climatic conditions and climate change scenarios (n = 433 nesting beaches; global climate datasets often are missing data for small islands, on which some sea turtle populations nest; Pike 2013a). To visualize these predictions in geographic space, I created maps showing the change in future hatching success relative to current predicted hatching success.

Results

Only 26.6% of loggerhead sea turtle nesting beaches worldwide are located in tropical latitudes (n = 248 of 933); the remaining 73.4% of nesting beaches are in temperate climates. Currently, ambient temperatures on loggerhead sea turtle nesting beaches located in tropical climates are significantly warmer than those located in temperate climates ($F_{1,475} = 98.64$, $P < 0.0001$; Fig. 1a). Tropical nesting beaches also produce significantly fewer hatchlings per nest than do temperate nesting beaches ($F_{1,19} = 7.19$, $P = 0.01$; Fig. 1b), providing strong support for a broad link between ambient temperatures and hatching success. These findings imply that climate change impacts on hatching success could be dependent upon how close current temperatures are to lethal, and the magnitude of local temperature increase. The effects of climate change on loggerhead sea turtles could thus differ regionally (temperate vs tropics), vary among spatially and biologically-distinct populations, and even among individual nesting beaches.

The quality of loggerhead sea turtle nesting habitat (as estimated by MaxEnt species distribution modeling) is significantly and positively related to empirical egg hatching success (logarithmic regression; n = 21 undeveloped nesting beaches, $R^2 = 0.525$, $F_{1,19} = 21.02$, $P = 0.0002$; Supporting Information Fig. S1). Habitat quality explains over 50% of the variation in hatching success among populations, and thus provides a strong measure of reproductive output. Hatching success was only weakly correlated with latitude, revealing that geographic location is a poor predictor of habitat quality ($R^2 = 0.12$, $F_{1,16} = 2.19$, $P = 0.160$).

Under current climatic conditions, loggerhead sea turtle nesting beaches do not frequently exceed temperatures that are lethal for incubating eggs (Godley *et al.* 2001; Katselidis *et al.* 2012); however, by 2080 the maximum temperature during the nesting season could exceed lethal levels at over half of tropical nesting beaches (Fig. 2). Under future climate change scenarios, a much lower proportion of temperate nesting beaches are expected to regularly exceed lethal temperatures as compared to tropical nesting beaches, despite both regions experiencing a similar magnitude of temperature increase (Fig. 2). This effect is because temperate nesting sites initially were cooler, and thus require a larger temperature increase to exceed lethal for developing embryos (Fig. 2). Under climate change, loggerhead turtles nesting in temperate environments are predicted to maintain high levels of hatching success overall, which could increase in those sites that have relatively low hatching success under the A1 and A2A future climate families for 2020-2080 (Fig. 3). By contrast, predictions from tropical nesting sites suggest that hatching success will decline overall during the same period (Fig. 3). The average predictions for all climate change scenarios produced remarkably similar hatching success estimates for both tropical and temperate locations within future time intervals (Fig. 2).

Nesting beach temperatures and hatching success show similar patterns between temperate and tropical nesting sites at even more local scales; individual spatially- and biologically-distinct populations in temperate locations generally have lower maximum temperatures and higher predicted hatching success than those in tropical locations (Fig. 1c). This pattern is also evident in the two individual populations that span both temperate and tropical latitudes (Fig. 1d). Overall, this strongly suggests that the impacts of climate change could differ substantially within and between populations, whether or not those populations are classified at local or regional scales.

Discussion

Understanding when, where, and how climate change will manifest, and to what degree, is crucial for ensuring the adequate conservation of imperiled species. One important, and understudied, aspect of climate change is how it will influence long-term population dynamics in terms of reproductive success, offspring production, and population demography. A necessary first step is an understanding of whether macro-scale environmental features contribute to successful reproduction, and how. The hatching success of loggerhead sea turtle eggs is strongly related to habitat quality, estimated using measures of seasonal variability in temperature and precipitation. Tropical nesting beaches experience significantly warmer ambient temperatures than do temperate beaches, and thus produce relatively fewer hatchling turtles per nest (Fig. 1). In some populations, climate change may not substantially alter hatching success of the eggs, whereas other populations could show either dramatic reductions or more complex responses, whereby hatching success initially increases with moderate warming but declines over the longer-term as warming continues (Fig. 3). These possible outcomes are likely a result of the wide geographic distribution across which loggerhead sea turtles nest, which is limited by physiological constraints of temperature and moisture on embryonic development (Pike 2013a). Overall, a regional conservation and management focus may be necessary to protect widespread and endangered species from climate change, which is difficult when populations span geopolitical boundaries across both terrestrial and marine environments (Wallace *et al.* 2010; Witt *et al.* 2010).

Visualizing hatching success in geographic space reaffirms broad differences in the hatching success of eggs from temperate and tropical loggerhead sea turtle populations; hatching success was generally predicted to be highest in temperate locations (e.g., southeastern United States, Mediterranean) and lowest in tropical locations (e.g., Central/South America, Australasia; Fig. 3). Hatching success in the Caribbean and

Australasian regions is not expected to show a marked change by 2020, whereas hatching success could increase in the Mediterranean Sea (Fig. 3). By 2050, however, hatching success is predicted to decline overall at many sites worldwide, which could continue through 2080 (Fig. 3). The Mediterranean Sea is predicted to have the largest geographic area showing an increase in hatching success, whereas the Caribbean and Australasian regions could show declines by more than 15% in some cases (Figs. 1-3). These patterns highlight some of the complex spatial, temporal, and population-specific impacts of climate change on reproduction in widespread species.

Although some of the predicted reductions in hatching success may not seem large (e.g., changes of a few percentage), other more subtle temperature effects on embryonic development could have strong and direct impacts on population characteristics. The sex of sea turtle embryos is determined by incubation temperature during development, and even slight increases in sand temperatures could alter population-specific sex ratios or other morphological characteristics (Fuentes & Porter 2013; Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Witt *et al.* 2010). This has led to speculation that some sea turtle nesting beaches will produce biased hatchling sex ratios, such that some geographic regions mainly produce males, and others mainly produce females (Fuentes & Porter 2013; Hawkes *et al.* 2007). The longer-term patterns of inter-annual variability in hatchling phenotype, and how these integrate over the extended generation time of sea turtles, are an important research area (Katselidis *et al.* 2012). Recent evidence from male turtles, however, suggests that their ability to breed annually with multiple females could help buffer any negative demographic consequences of skewed adult sex ratios (Hays *et al.* 2010; Wright *et al.* 2012).

Habitat quality, generated using maximum entropy relationships among temperature and precipitation, explained more than half of the variation in hatching success among loggerhead sea turtle populations globally. This is exceptional explanatory power when considering that local factors intrinsic to characteristics of the mother and nesting habitat influence nest temperature, including patterns of nest-site selection (e.g., by females selecting for sand albedo, aspect, slope, or other factors among and within beaches; Hays *et al.* 1995, 2001; Wood & Bjorndal 2000). Nest depth also plays important roles in incubation temperature, which in turn directly influences hatching success and hatchling sex and phenotype (Ackerman 1997). Although current research has yet to tackle how these aspects influence microclimatic conditions within nests worldwide, recent advances in mechanistic modeling approaches may offer one potential solution (Fuentes & Porter 2013). Mechanistic modeling also can be used to predict much more subtle seasonal effects of nest temperature on hatchling fitness, to better integrate predictions of these variables over timescales relevant to sea turtle ecology (e.g., decades). At present, however, our understanding of how climate variability will impact the temporal pace of hatchling production and phenotype is limited to broad predictions averaged over discrete time intervals. More subtle seasonal and inter-annual patterns have, to date, received little research attention, but this natural variation has the potential to buffer the impacts of climate change (Katselidis *et al.* 2012). Likewise, testing climate change predictions is essential to refining models to increase explanatory power. The hatching success predictions that I have generated can now be tested against field data and refined as empirical datasets become available and climate change predictions are updated. Although published data on hatching success are lacking for other sea turtle species (Pike 2008, 2009), these results provide a baseline prediction for other species because current evidence suggests that sea turtles have fixed thermal reaction norms (Ackerman 1997).

Females of most oviparous species are selective in where they place their eggs, favouring microhabitats that will reduce hatching time and maximize hatching success and offspring fitness (e.g., warmer nest temperatures; Huang & Pike 2011). This has led to speculation that nesting females could compensate for the effects of climate change by continuing to locate microhabitats that maximize fitness (Mitchell *et al.* 2008; Telemeco *et al.* 2009, 2013). The sandy, sun-exposed beaches upon which sea turtles nest can experience high temperatures (Katselidis *et al.* 2012; Tapilatu & Tiwari 2007), but we do not yet understand whether maternal nest-site selection could compensate for temperature increases under climate change. Data from other, smaller reptile species that dig shallower nests suggest that morphological constraints on the ability to dig deeper nests could limit potential adaptive responses to climate change, and lead to skewed sex ratios and increased embryonic mortality (Katselidis *et al.* 2012; Mitchell *et al.* 2008; Telemeco *et al.* 2013). This is also a concern in sea turtles (Katselidis *et al.* 2012), although their ability to dig extremely deep nests (>1m below the surface) could provide a mechanism by which females can buffer their developing offspring from climate change (Mitchell *et al.* 2008; Telemeco *et al.* 2013).

Conclusions

The most direct impacts of climate change will come from the interactive effects of multiple stressors, which for many ectotherms will be the diverse impacts of temperature on all aspects of life history and ecology. Integrating the varied effects of temperature on embryonic survival, hatchling phenotype, and habitat use of marine life stages with other stressors is the only way to effectively prepare for the ecological effects of climate change. Doing this collectively within a single modeling framework is extremely difficult due to the complexity of responses at different spatial and temporal scales for the different life stages. An alternative approach may be to integrate the body of accumulating information on different threats using a vulnerability assessment framework or resilience indices (e.g., Fuentes *et al.* 2011, 2013). Novel integration of disparate predictions of climate change and anthropogenic stressors are crucial towards a fuller understanding of how we are changing the face of biodiversity.

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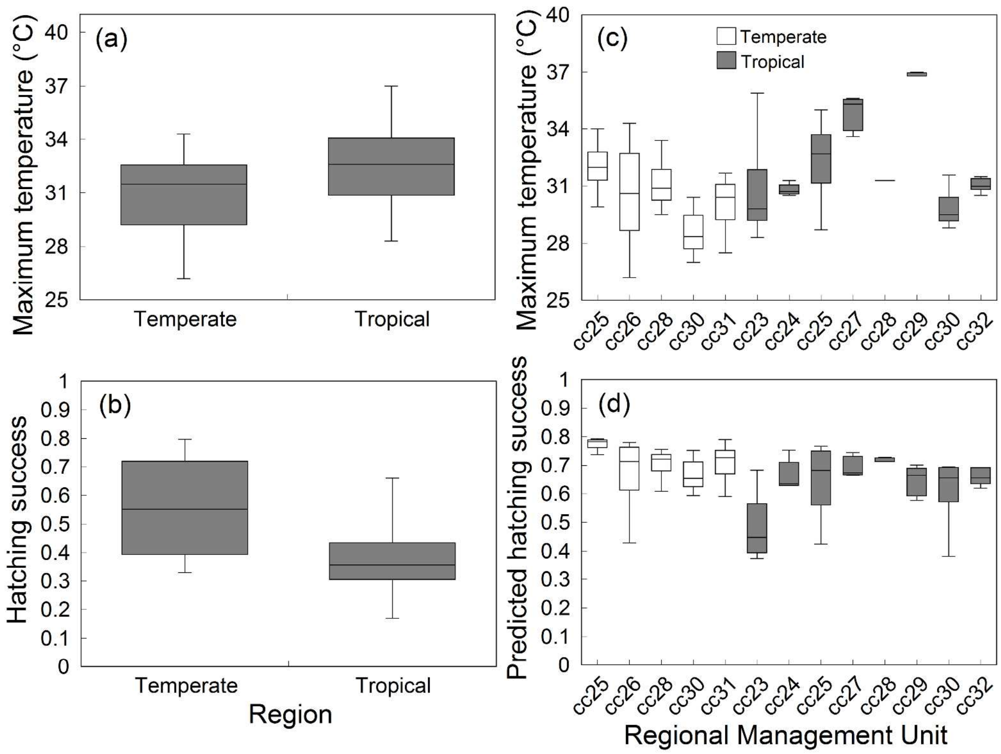
Figure Legends

Figure 1: Maximum temperatures during the warmest quarter of the year (summer, when many sea turtle populations are nesting) are higher on tropical beaches than on temperate beaches (a) and are higher on tropical Regional Management Unit (Wallace *et al.* 2010) beaches than on temperate Regional Management Unit beaches (c). Data from the literature reveal that loggerhead nests from temperate regions have higher hatching success than those laid on tropical nesting beaches (b). Median hatching success of temperate beaches is 28.7% higher than tropical beaches. Predictions of hatching success generated from Maxent modeling were higher for temperate Regional Management Unit beaches than for tropical Regional Management Unit beaches (c). The lower bound of each box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.

Figure 2: Change in predicted (a) maximum temperature during the warmest quarter of the year (summer, when many sea turtle populations are nesting) and (b) hatching success, averaged under climate change emission families and shown for tropical and temperate nesting beaches. The lower bound of each box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.

Figure 3: Maps forecasting loggerhead turtle hatching success and the change in hatching success under climate change, both spatially (Caribbean Sea, Mediterranean Sea, and Australasia) and temporally (under current and future predicted climates). Shown across the top row are predictions of hatching success under current climatic conditions (divided into six quantiles) and the remaining panels show changes in hatching success relative to current

conditions (divided into 5% intervals). Negative values indicate a decline in hatching success and positive values indicate an increase hatching success under future conditions. Future conditions were averaged among the different emission scenarios, resulting in one prediction for each of 2020, 2050, and 2080. Hatching success was predicted using the regression equation from the relationship between habitat suitability (estimated through MaxEnt modeling) and empirical hatching success.



Maximum temperatures during the warmest quarter of the year (summer, when many sea turtle populations are nesting) are higher on tropical beaches than on temperate beaches (a) and are higher on tropical Regional Management Unit (Wallace et al., 2010) beaches than on temperate Regional Management Unit beaches (c). Data from the literature reveal that loggerhead nests from temperate regions have higher hatching success than those laid on tropical nesting beaches (b). Median hatching success of temperate beaches is 28.7% higher than tropical beaches. Predictions of hatching success generated from Maxent modelling were higher for temperate Regional Management Unit beaches than for tropical Regional Management Unit beaches (c). The lower bound of each box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.
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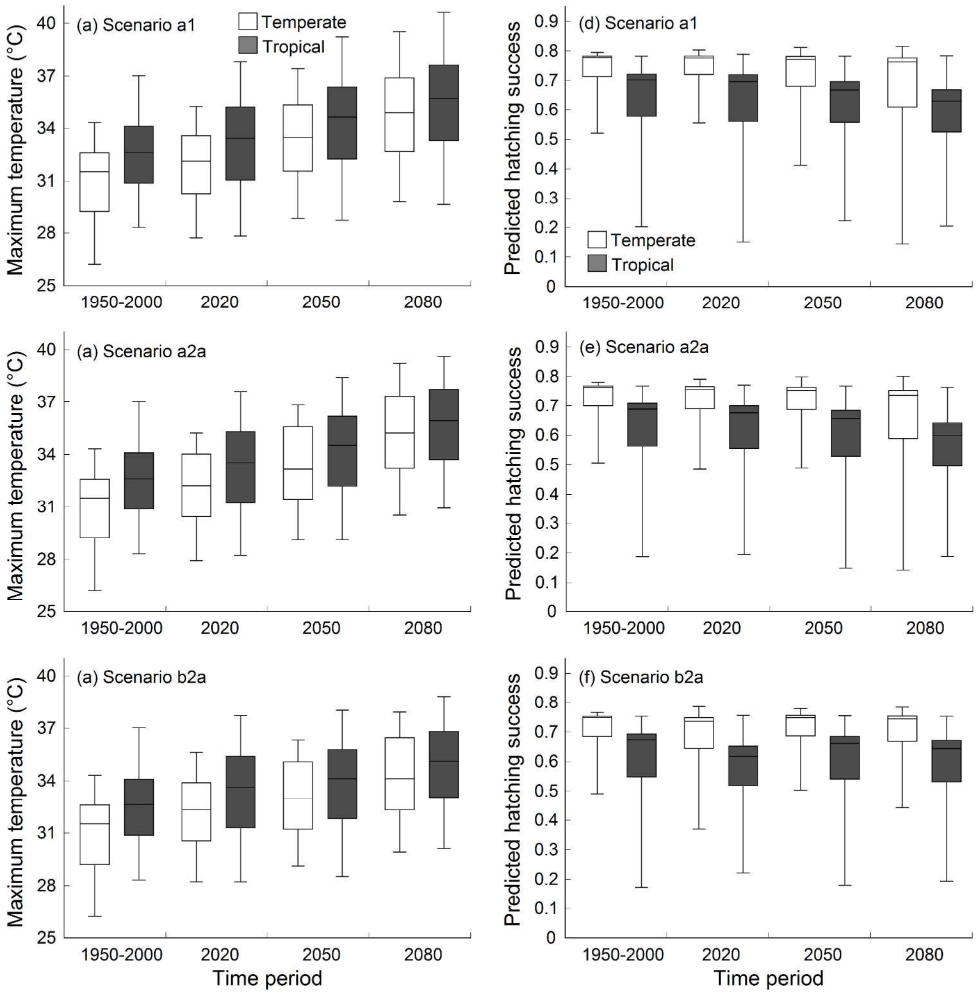

Change in predicted (a) maximum temperature during the warmest quarter of the year (summer, when many sea turtle populations are nesting) and (b) hatching success, averaged under climate change emission families and shown for tropical and temperate nesting beaches. The lower bound of each box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.
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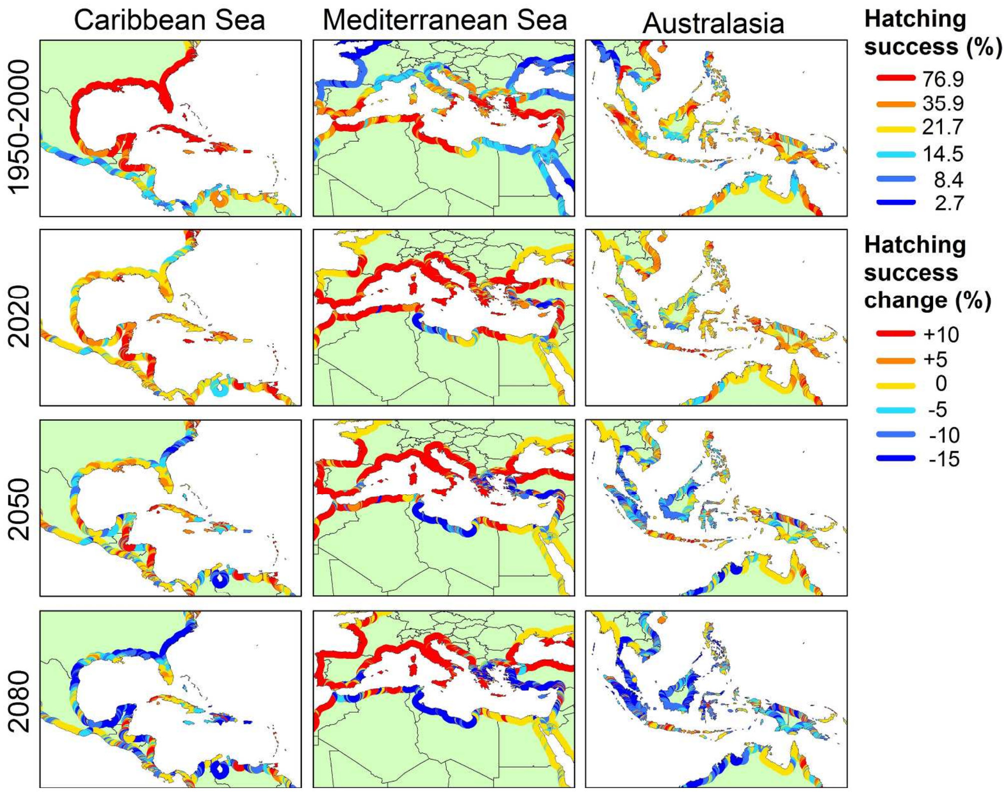

Maps forecasting loggerhead turtle hatching success and the change in hatching success under climate change, both spatially (Caribbean Sea, Mediterranean Sea, and Australasia) and temporally (under current and future predicted climates). Shown across the top row are predictions of hatching success under current climatic conditions (divided into six quantiles) and the remaining panels show changes in hatching success relative to current conditions (divided into 5% intervals). Negative values indicate a decline in hatching success and positive values indicate an increase hatching success under future conditions. Future conditions were averaged among the different emission scenarios, resulting in one prediction for each of 2020, 2050, and 2080. Hatching success was predicted using the regression equation from the relationship between habitat suitability (estimated through MaxEnt modeling) and empirical hatching success.
229x180mm (300 x 300 DPI)