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Colonization of new nesting areas could provide climate refuge to loggerhead turtles under climate change

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A R T I C L E I N F O

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A B S T R A C T

Climate change can impact regional and global biodiversity for multiple reasons. In sea turtles, changes in local climate at nesting beaches can affect egg and hatchling survival and primary sex ratios. Sea turtles could respond to climate change by occupying new nesting areas. The recent increase in sporadic nesting in the western Mediterranean may indicate colonization of new nesting beaches. We assessed the suitability of a western area, the Balearic Islands (~1500 km from current nesting grounds) as climate refuge for loggerhead turtles (*Caretta caretta*) under current (2015–2017) and climate change scenarios to the mid (+40 years) and end (+80 years) of the 21st century. Using a correlative approach based on air and sand temperatures, we predicted nest temperatures and sex ratios for 19 beaches. Most beaches could provide viable temperatures and predominantly produce male hatchlings under all scenarios. Sex ratio projections were male-biased but with an increasing female ratio throughout time. Although mean sex ratio under the +80 years scenario was still male-biased, the warmest beaches could provide female-biased ratios, which are similar to those estimated for current nesting sites. The Balearic Islands could function as climate refuge for loggerhead turtles in the Mediterranean because temperatures could favor embryo viability and a male sex ratio. However, a nesting population may not be established until the percentage of female hatchlings increases and turtles return to nest as adults. Conditions at sea should also favor survival of hatchlings and juveniles. Because western Mediterranean beaches are popular tourist destinations, active management may be needed to protect nesting populations.

1. Introduction

Climate change can potentially reduce biodiversity by impacting species directly or by exacerbating other ongoing threats (Brook et al., 2008). Its negative effects on many species has received considerable attention within the scientific community (Butler, 2018). However, major climate changes have previously occurred in the history of Earth during which, some species went extinct but many others survived (Nogués-Bravo et al., 2018). The survival of many species through climate crises indicates that species have some mechanisms of resilience against short- or long-term detrimental climatic conditions (Gaillard et al., 1998; Parmesan, 2006). However, the current rate of warming could also surpass their capacity for adaptation (Visser, 2008; Santidrián Tomillo et al., 2015). Mechanisms to adapt could imply physiological changes toward increasing thermal tolerances (Brook et al., 2008) or behavioral changes such as phenological shifts to reproduce during the most favorable times (Iler et al., 2021) and spatial shifts to colonize new areas (Parmesan, 2006).

In oviparous species that lack parental care, changes in the surrounding physical environment could largely impact embryos because a successful development depends on suitable climatic conditions (Sun et al., 2021). Sea turtles in particular, bury their eggs on sandy beaches

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that provide relatively stable conditions of temperature and humidity (Ackerman, 1997). However, eggs normally only develop within a viable range of temperatures (~25–35 °C, Ackerman, 1997), and are even vulnerable to high temperatures within that range (Santidrián Tomillo et al., 2017). While the detrimental effect of high temperatures on sea turtle embryo and hatchling survival has been found in several populations (Santidrián Tomillo et al., 2012; Valverde et al., 2010), little attention has been paid to the arise of new nesting beaches that could become optimal for egg incubation as temperatures get warmer.

Sea turtles have temperature-dependent sex determination type Ia such that embryos develop into female hatchlings at higher temperatures and into males at lower temperatures (Standora and Spotila, 1985). Primary sex ratios in sea turtles are typically female-biased (Godfrey et al., 1996, 1999). Although rare, extremely female-biased sex ratios have also been found in some populations (Broderick et al., 2000). As further feminization is likely to occur at the warmest end of the nesting range of a population, the colonization of cooler nesting areas could guarantee the production of males and in some cases, higher hatching success. Thus, male-producing nesting beaches could become critical for sea turtle populations under climate warming (Hawkes et al., 2007), since both male and female turtles are needed for population sustainability.

Sea surface temperature (SST) also affects the rate of maturation of eggs in the female oviduct of sea turtles. Threshold temperatures for egg maturation in the female oviduct are around 22 °C with more favorable conditions at higher temperatures (Hays et al., 2002; Schofield et al., 2009, 2021). The number of days elapsed between consecutive nesting attempts, known as the inter-nesting period, is also affected by water temperature, being shorter at higher temperatures (Weber et al., 2011; Valverde-Cantillo et al., 2019). In temperate areas, where the nesting window is shorter because it is limited to the summer, longer inter-nesting periods could potentially reduce the number of clutches that turtles can lay within the nesting season (Schofield et al., 2009, 2021). Thus, seawater warming could potentially facilitate the colonization of new nesting beaches.

The colonization of sea turtle nesting beaches has not been described in present times, as the process is necessarily slow in species with deferred breeding. However, the occurrence and timing of past colonization events have been pinpointed through genetic studies (Bowen and Karl, 2007; Baltasar-Soares et al., 2020). The study of genetic diversity of loggerhead turtles (*Caretta caretta*) for instance, has showed that Mediterranean loggerhead turtles originated from the Atlantic Ocean (Clusa et al., 2013), with some individuals later recolonizing islands of the Atlantic (Baltasar-Soares et al., 2020). Coming back to the present, it has been suggested that the increasing number of sporadic nesting events in the western Mediterranean in recent years may be an early sign of colonization (Maffucci et al., 2016; Carreras et al., 2018; Hochscheid et al., 2022). Current climatic conditions in the western basin are cooler than in the eastern one but have become suitable for nesting, at least during the core of the nesting season (Santidrián Tomillo et al., 2022). Thus, western nesting areas could potentially serve as climate refuge for Mediterranean loggerhead turtles if climatic conditions in other parts of the Mediterranean Sea became detrimental. In Greece, loggerhead turtles nest when water temperatures are above 22 °C, but conditions are optimal for nesting at SSTs between 26 and 29 °C (Schofield et al., 2009, 2021). Current SSTs in western areas reach temperatures above the 22 °C threshold during the peak of the summer (July–August), but are still generally below optimal levels (Santidrián Tomillo et al., 2022).

We propose that new nesting beaches could contribute to mitigate the impact of climate change by progressively providing more optimal conditions (1) at sea for egg maturation in the female oviduct and (2) on the beaches for egg incubation and by favoring the production of a greater percentage of male turtles than those of warmer sites. We test this hypothesis by studying current and future thermal conditions provided by the beaches and surrounding waters of the Balearic Archipelago, Spain, an emerging nesting area for loggerhead turtles in the Mediterranean. By projecting nest temperatures, SSTs and sex ratios throughout the 21st century, we assessed the suitability of this western area to serve as a climate refuge for loggerhead turtles in the Mediterranean.

2. Methods

2.1. Study site

We conducted the study at the four main islands of the Balearic Archipelago: Mallorca, Menorca, Ibiza and Formentera (Fig. 1). Loggerhead turtle nesting attempts have been recorded at the Balearic Islands since 2015 and successful nesting since 2019. Attempts have occurred at all islands, except in Mallorca. Since Mallorca is the largest island in the Archipelago and the lack of nesting records could be explained by the low nesting frequency in the area and/or low detection effort, we included it in the study, as a future potential nesting site.

We studied thermal conditions of 19 beaches. Seven of these were located in Mallorca (Palma, Ses Covetes, S'Amarador, Sa Canova, Cala Mesquida, Tora Paguera and Sa Coma), six in Menorca (Algaiarens, Atalis, Cala Tirant, Cala Mesquida, Binibequer and Son Saura), four in Ibiza (Ses Salines, Es Cavallet, Cala Tarida and Portinatx) and two in Formentera (Es Pujols and Migjorn) (Fig. 1).

2.2. Current thermal conditions

We placed dataloggers Onset Hobo Tidbit v2 (±0.2 °C) at the depth of a loggerhead nest (c. 40 cm) (based on Zbinden et al., 2006). All loggers were placed at the same depth to infer what the temperature in the center of a standard clutch of eggs could be. Because the only source of heat in a nest is the insolation of the beach surface, we consider that this experimental setup was appropriated to simulate incubation temperature of a clutch of eggs (0.5 °C was added to account for the metabolic heating of a nest, see below). Dataloggers collected data between June 1st and September 30th at 30 min intervals over three nesting seasons (2015, 2016 and 2017). We intercompared all dataloggers before and after the field study and exposed them to temperatures within the typical ranges of sand temperatures. If dataloggers differed on average by >0.3 °C they were excluded from the study. We placed a single datalogger per beach at the same location every year to capture inter-annual variability, with the exception of two beaches: Son Saura, which was not monitored in 2017 and Portinatx, which was only monitored in 2017. In all cases, we placed the dataloggers in a wide open area of the beach above the high tide line where the risk of inundation was very low.

Sand and nest temperatures have been found to be highly correlated with air temperatures on many nesting beaches (Laloë et al., 2014; Laloë et al., 2021). Precipitation has also been found to influence nest temperatures at some locations, especially in tropical areas (Houghton et al., 2007; Esteban et al., 2016). Thus, to assess the influence of local climatic conditions on nest temperatures, we compared daily sand temperatures obtained from the dataloggers at each beach to the daily air temperature and precipitation obtained from a weather station located on the corresponding island. The weather stations were located at Palma de Mallorca port (39.5556, 2.6264), Menorca airport (39.8544, 4.2156) and Ibiza airport (38.8764, 1.3842). Local climate data were freely available at the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration of the USA (https://www.ncdc.noaa.gov/cdo-web/). Because we had no climatic data for Formentera, we used data from the Ibiza weather station for Es Pujols and Migjorn beaches, which were located at distances of 18 km and 25 km from the Ibiza weather station respectively.

We tested for normality in the temperature data obtained from the dataloggers with a Shapiro test. Because data were not normally distributed, we used a Kruskall-Wallis with a posthoc pairwise Wilcox test, Bonferroni adjusted to assess for differences in sand temperature

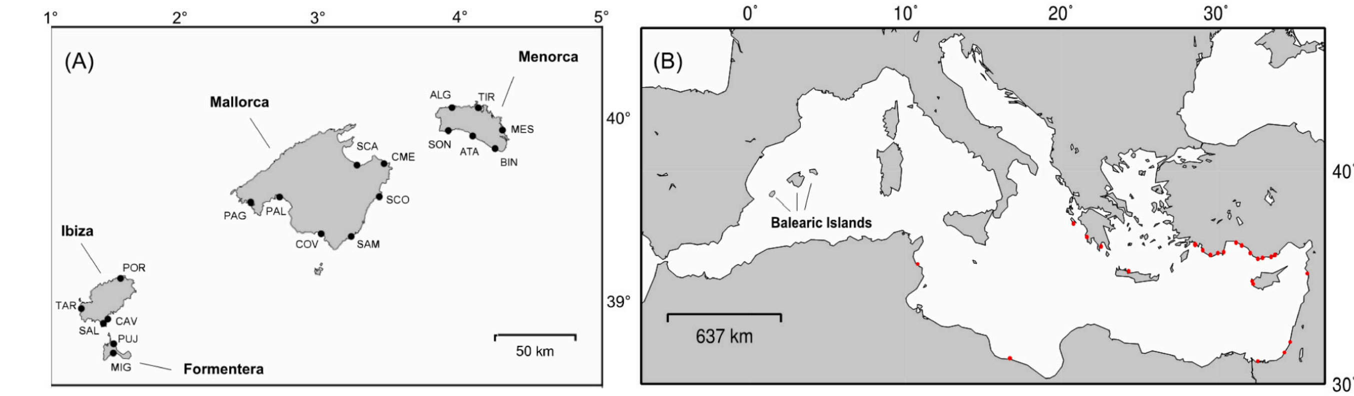

Fig. 1. (A) Location of the beaches of the Balearic Islands where sand temperatures were recorded: Palma (PAL), Ses Covetes (COV), S'Amarador (SAM), Sa Coma (SCO), Cala Mesquida (CME), Sa Canova (SCA) and Tora Paguera (PAG) in Mallorca, Atalis (ATA), Son Saura (SON), Binibequer (BIN), Sa Mesquida (MES), Cala Tirant (TIR) and Algaiarens (ALG) in Menorca, Cala Tarida (TAR), Ses Salines (SAL), Es Cavallet (CAV) and Portinatx (POR) in Ibiza and Migjorn (MIG) and Es Pujols (PUJ) in Formentera. (B) Location of the Balearic Islands in relation to current loggerhead nesting areas (red circles) in the Mediterranean, based on Camiñas et al., 2020. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

among beaches, islands, months of the season, and years. We also compared mean daily sand temperatures for each beach to the mean, maximum and minimum daily air temperatures and precipitation. We considered linear and quadratic relationships, as well as generalized linear models (GLM) and generalized additive models (GAM). However, since GLM and GAMs were practically identical to linear regressions, these were excluded. We used the Akaike Information Criterion to select the models that better explained changes in sand temperature (lowest AIC value). We used R version 4.1.2 to perform all statistical analyses.

2.3. *Projections of local climate, nest temperatures and sex ratios under climate change scenarios*

We obtained high-resolution projections of monthly sea surface temperature (SST), surface air temperature and precipitation for the Balearic Islands under a climate change scenario of a 1 % per year increase in atmospheric CO_2 (called a transient climate response in the IPCC reports) in NOAA GFDL's global climate model CM2.6 (IPCC, 2021). The resolution of the CM2.6's ocean component (SST) was 10-km and its atmosphere component (air temperature and precipitation) was 50-km. The area encompassed the whole Archipelago (between 40.5°N, 38.5°N, 1°E and 5°E) (Fig. 2). The climate projections provided data as deltas. In the case of air temperatures and SSTs, we added the deltas to the mean temperatures recorded at each island each month over the 2000–2020 period to obtain the actual projected air and water temperatures.

The results of the analysis on the effect of local climate on sand temperature indicated that sand temperature was highly correlated to air temperature and that precipitation did not affect it or had a very small effect (Table S2). Thus, to obtain projections on sand/nest temperatures throughout the 21st century from the projections on air temperatures, we applied the regression equation that best explained the relationship between air and sand temperatures for each beach (Table S2). We projected sand temperatures to the middle (+40 years) and end (+80 years) of the 21st century. Because the projections of precipitation did not significantly change throughout the 21st century in this region, we considered that the relationship between sand and air temperatures would remain consistent throughout this time.

We compared the predicted values to the actual values of sand temperatures for the three years we had data (2015, 2016 and 2017) to bias-correct our projections. We did this by estimating the mean difference between the observed and predicted values for each beach and each month and added this difference to the predictions (Table S3). Nest temperatures were finally inferred from sand temperatures by adding 0.5 °C to account for the metabolic heating generated by the developing embryos (Godley et al., 2001).

Sex ratios were estimated for the months when eggs could be incubating and we considered that the thermosensitive period for sex determination (middle third of development) would occur in June, July, August and September. We estimated mean sex ratios under three time-periods (current conditions, +40 years, + 80 years). We used the relationship between mean nest temperature and sex ratio described for the loggerhead turtles that nest in Greece (TSD curve described in Rees and Margaritoulis, 2004, based on Mrosovsky et al., 2002) to allocate a sex ratio (female percentage) to each nest temperature. This TSD-curve has approximately a pivotal temperature and a transitional range of temperatures around 29.7 °C and between 29.0 °C and 30.5 °C respectively (Rees and Margaritoulis, 2004).

We estimated mean sex ratio based on the mean nest temperature and standard deviation (SD) for each beach and each month. We recreated stochasticity by picking a random value of temperature within the SD limits of the mean. Based on the TSD-curve, a sex ratio was assigned to that value of temperature. This process was repeated 1000 times and the mean sex ratio was estimated by averaging the 1000 assigned sex ratio values. We used the lnorms and ifelse functions of library popbio (Stubben and Milligan, 2007) in R to infer sex ratios this way.

3. Results

3.1. *Current conditions*

There were statistically significant differences in mean, maximum and minimum sand temperatures between islands, beaches, months and years ($p < 0.001$ all cases, Table S1). Sand temperatures at nest depth were highest in Ibiza, followed by Formentera (Table 1, Fig. 3). The pairwise comparisons indicated that differences in mean, maximum and minimum sand temperatures between islands were statistically significant in all cases ($p < 0.001$).

There were also differences in sand temperatures among beaches. Mean sand temperatures were below the lower thermal limit for egg development in 6 of the 19 beaches. Four of these beaches were located in Mallorca (Ses Covetes, S'Amarador, Sa Canova and Sa Coma) and two in Menorca (Binibequer and Son Saura). Warmest temperatures were recorded at three beaches in Ibiza (Cala Tarida, Portinatx and Ses Salines). However, mean sand temperatures at the warmest beach in Mallorca (Palma) and the warmest beach in Menorca (Sa Mesquida) were only slightly lower than those in Ibiza (all above 27 °C) (Table 2) and with no statistically significant differences between them (except in between Palma and Cala Tarida).

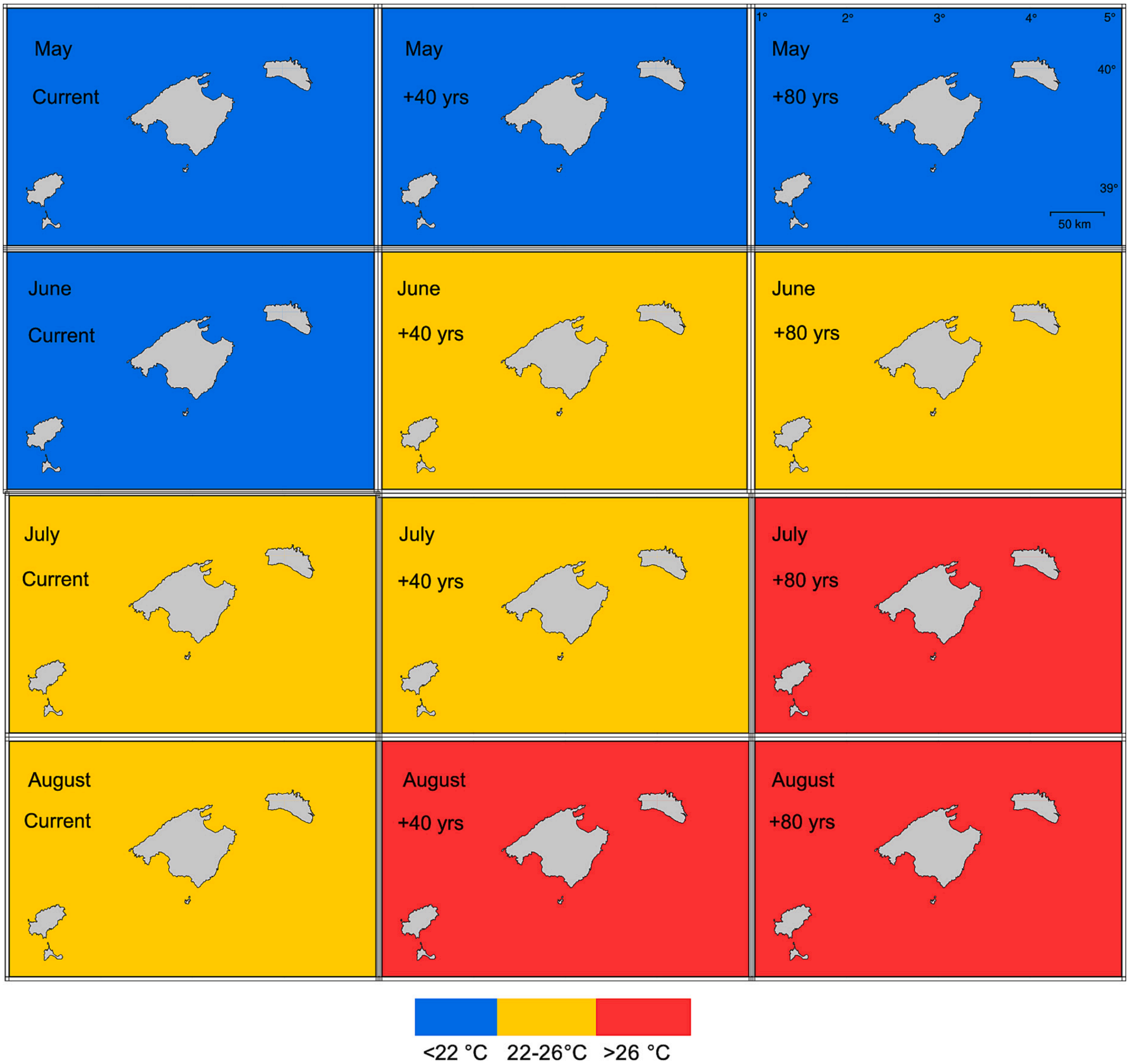

Fig. 2. Sea Surface Temperatures (°C) around the Balearic Archipelago under current and projected conditions (at +40 years and + 80 years) during the potential nesting season (May, June, July and August) of loggerhead turtles (*Caretta caretta*). We considered conditions for nesting are below suitable for nesting at temperatures below 22 °C (blue in figure), suboptimal between 22 °C and 26 °C (yellow) and optimal above 26 °C (red), based on Schofield et al. (2009, 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mean, maximum and minimum empirical sand temperatures at 40 cm per month (June to September), year (2015, 2016 and 2017) and island (Mallorca, Menorca, Ibiza and Formentera) for 19 beaches of the Balearic Archipelago.

		Tmean	Tmax	Tmin
Month	June	24.5 ± 1.9	24.9 ± 2.2	24.1 ± 2.0
	July	26.9 ± 1.8	27.1 ± 1.8	26.7 ± 1.8
	August	27.1 ± 1.7	27.3 ± 1.7	26.9 ± 1.8
	September	24.9 ± 2.0	25.2 ± 2.0	24.6 ± 2.0
Island	Formentera	26.9 ± 1.5	27.1 ± 1.5	26.6 ± 1.7
	Ibiza	27.4 ± 1.6	27.7 ± 1.7	27.2 ± 1.7
	Mallorca	25.1 ± 2.1	25.4 ± 2.1	24.9 ± 2.1
	Menorca	25.4 ± 2.3	25.7 ± 2.3	25.1 ± 2.3
Year	2015	26.1 ± 2.3	26.4 ± 2.4	25.8 ± 2.4
	2016	25.4 ± 2.0	25.6 ± 2.0	25.1 ± 2.0
	2017	26.1 ± 2.3	26.4 ± 2.2	25.9 ± 2.3

Mean temperatures in June and September were below the lower thermal limit for egg development (25 °C) and were ~ 2.0–2.5 °C lower than in July and August ($p < 0.01$ in all cases) (Table 1). Mean, maximum and minimum sand temperatures were statistically significantly warmer in August than in July and in July than in the other two months. There were also differences in sand temperatures among years, being statistically significantly lower in 2016 than in 2015 and 2017 (Table 1) ($p < 0.001$), but with no differences between 2015 and 2017 ($p = 0.2$ and $p = 0.9$ for mean and maximum temperatures respectively), except in minimum temperatures ($p = 0.049$).

Linear regression models using mean air temperature as a predictor for sand temperature were generally the best models. The R^2 was above 0.50 in most cases except for Son Saura ($R^2 = 0.16$, Table S2). Precipitation only influenced sand temperature at four beaches, three of which were in Menorca (Algaiarens, Atalis and Son Saura) and one in Mallorca (Palma), but the contribution of precipitation to the models was minimal (Table S2). At six beaches, minimum temperatures were better predictors of sand temperatures than mean temperatures. However, differences between these and the mean temperatures models were also very small. Quadratic regression using mean air temperature as predictor were statistically significant for five beaches (Son Saura, Es Cavallet, Es Pujols, Portinatx and Ses Covetes) (Table S2). As before, the

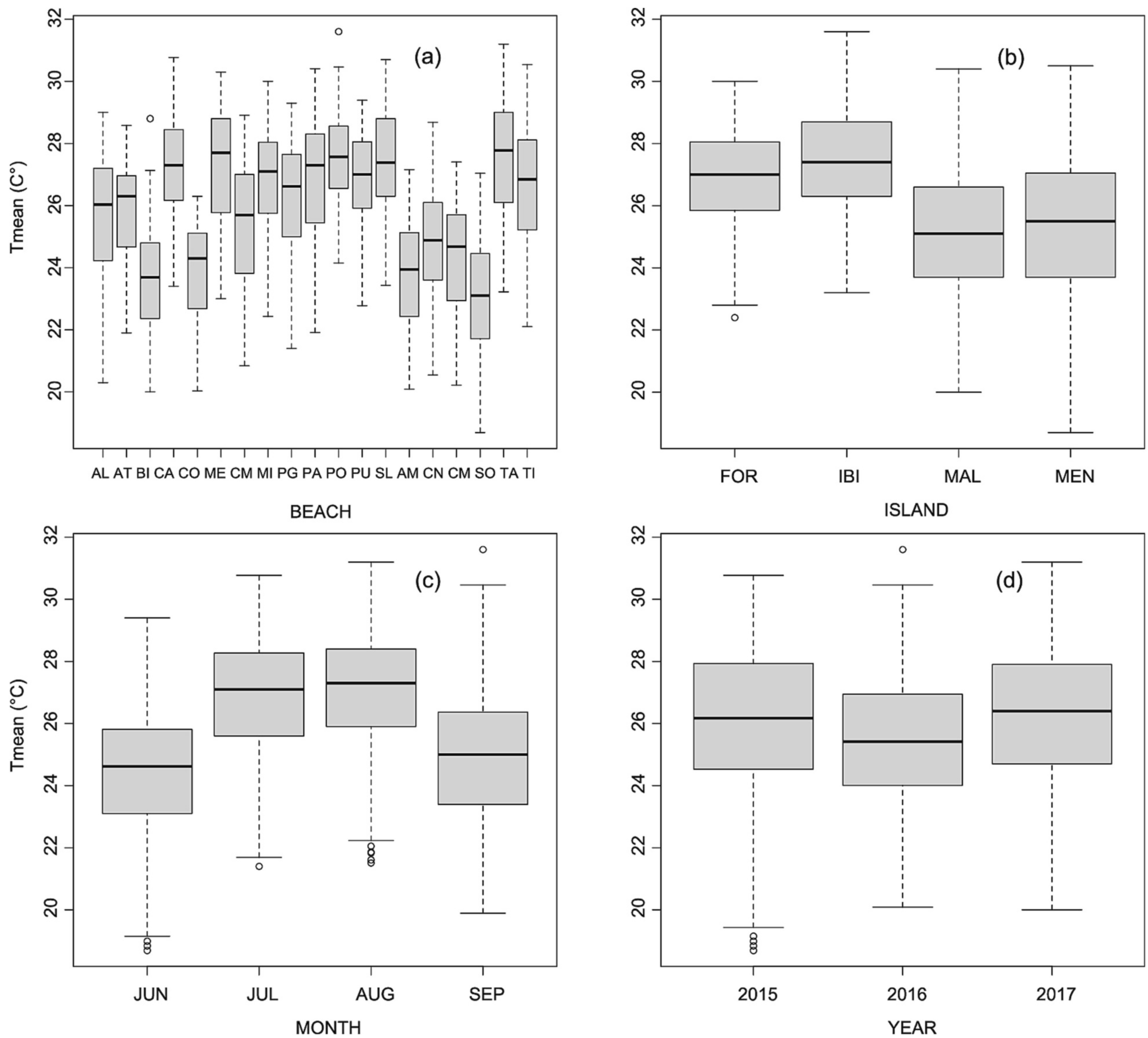

Fig. 3. Current conditions of mean sand temperatures (°C) at 40 cm by (a) beach, (b) island (Mallorca, Menorca, Ibiza and Formentera), (c) month (June – September) and (d) year (2015–2017). Beaches monitored were Algaiarens (AL), Atalis (AT), Binibequer (BI), Es Cavallet (CA), Ses Covetes (CO), Sa Mesquida (ME), Cala Mesquida (CM), Migjorn (MI), Tora Paguera (PG), Palma (PA) Portinatx (PO), Es Pujols (PU), Ses Salines (SL), S'Amarador (AM), Sa Canova (CN), Sa Coma (CM), Son Saura (SO), Cala Tarida (TA), Cala Tirant (TI).

quadratic models were also similar to the linear ones. The difference between observed sand temperatures and predicted temperatures based on the GFDL model varied among beaches and months. The largest differences between observed and predicted sand temperatures were found for June (mean ± SD: 0.76 ± 0.24 °C), followed by August (−0.54 ± 0.15 °C) and July (−0.18 ± 0.19 °C) and the smallest differences were found for September (−0.01 ± 0.31) (Table S3).

3.2. Climate change projections: local climate and nest temperatures

The climatic projections from the NOAA GFDL model indicated that both air temperatures and SSTs are projected to increase throughout the 21st century particularly after 2060 and especially in July and August (Fig. 4). Mean temperatures during the nesting season are projected to increase by 1.8–2.6 °C and by 1.6–2.3 °C in land (air temperature) and the sea respectively. Precipitation, on the contrary, is projected to remain similar to current conditions with small changes in monthly levels between −8.0 to +6.4 mm (Fig. 4).

Sea surface temperatures in May are projected to remain below the thermal threshold for egg maturation in the female oviduct (22 °C) under all scenarios. In June, July and August, conditions at sea are projected to become more favorable for egg maturation throughout time. In particular, conditions are projected to change from below the thermal threshold to suboptimal levels (above 26 °C) under the +40 years scenario in June, from suboptimal to optimal conditions under the +80 years scenario in July and from suboptimal to optimal conditions under the +40 years scenario in August (Fig. 2).

Nest temperatures are also projected to increase throughout the 21st century (Fig. 5). Nevertheless, almost half of the beaches were projected to have mean temperatures below the thermal limit for egg development (25 °C) in June and September. On the contrary, temperatures in July and August are projected to be above the thermal limit for egg development in most beaches, and in all beaches but one by the end of the 21st century (Fig. 5, Table 3). Mean temperatures in June were also projected to be below the transitional range of temperatures (TRT) that produces both sexes in all beaches throughout the 21st century. In September, projections only periodically reached temperatures within the TRT at the warmest beaches and during the warmest years. In July

Table 2
Mean, maximum and minimum empirical sand temperature per beach at 40 cm at the Balearic Islands (Mallorca, Menorca, Ibiza and Formentera). Temperatures were monitored between June 1st and September 30th of 2015, 2016 and 2017. Beaches monitored were Algaiarens (ALG), Atalis (ATA), Binibequer (BIN), Es Cavallet (CAV), Ses Covetes (COV), Sa Mesquida (MES), Cala Mesquida (CME), Migjorn (MIG), Tora Paguera (PAG), Portinatx (POR), Es Pujols (PUJ), Ses Salines (SAL), S'Amarador (SAM), Sa Canova (SCA), Sa Coma (SCO), Son Saura (SON), Cala Tarida (TAR), Cala Tirant (TIR) and Palma (PAL).

Beach	Island	Tmean	Tmax	Tmin
ALG	Menorca	25.7 ± 2.0	26.1 ± 2.0	25.3 ± 2.1
ATA	Menorca	25.9 ± 1.5	26.1 ± 1.6	25.6 ± 1.6
BIN	Menorca	23.6 ± 1.6	24.0 ± 1.7	23.3 ± 1.6
CAV	Ibiza	27.3 ± 1.6	27.5 ± 1.6	27.0 ± 1.8
COV	Mallorca	23.9 ± 1.6	24.1 ± 1.5	23.7 ± 1.6
MES	Menorca	27.3 ± 1.8	27.6 ± 1.8	26.9 ± 2.0
CME	Mallorca	25.5 ± 1.9	25.6 ± 1.9	25.3 ± 1.9
MIG	Formentera	26.8 ± 1.6	27.1 ± 1.5	26.6 ± 1.7
PAG	Mallorca	26.3 ± 1.7	26.7 ± 1.7	25.9 ± 1.7
PAL	Mallorca	27.0 ± 1.9	27.2 ± 1.8	26.7 ± 1.9
POR	Ibiza	27.5 ± 1.4	27.8 ± 1.7	27.2 ± 1.4
PUJ	Formentera	26.9 ± 1.4	27.1 ± 1.5	26.7 ± 1.4
SAL	Ibiza	27.4 ± 1.6	27.7 ± 1.7	27.2 ± 1.7
SAM	Mallorca	23.8 ± 1.8	24.0 ± 1.8	23.6 ± 1.8
SCA	Mallorca	24.8 ± 2.0	25.0 ± 2.0	24.6 ± 2.0
SCO	Mallorca	24.4 ± 1.6	24.8 ± 1.8	24.1 ± 1.7
SON	Menorca	23.1 ± 1.8	23.4 ± 1.9	22.8 ± 1.7
TAR	Ibiza	27.6 ± 1.8	27.9 ± 1.7	27.4 ± 1.8
TIR	Menorca	26.7 ± 2.0	26.9 ± 2.0	26.4 ± 2.1

and August, most beaches were projected to have temperatures below the TRT. However, several beaches could consistently reach temperatures within the TRT, with a tendency to increase over time and even to temperatures above the TRT toward the end of the 21st century (Fig. 5).

3.3. Climate change projections: sex ratios

The proportion of female hatchlings that could be produced at the Balearic Islands is projected to increase throughout the 21st century (Fig. 6). However, only a few beaches are projected to provide thermal conditions that could allow the production of both sexes, even under the warmest scenario. Projections show that the beaches of the Balearic Islands could produce no female hatchlings in nests for which sex determination occurs in June and very few female hatchlings in nests when sex determination is occurring in September. In July, the mean sex ratio could remain at ~9 % female in +40 years but could increase to ~36 % in +80 years. In August, mean sex ratio could change from ~11 % to ~24 % in +40 years and to ~38 % in +80 years (Fig. 6). Even if mean sex ratios were projected to be male-biased under all scenarios, sex ratios at the warmest beaches of the Balearic Islands could be female-biased under the +80 years scenario in July and August (Table 3, Fig. 6), reaching levels that are similar to those currently estimated for well-established nesting populations around the world. In particular, no beaches in any month would be above 50 % female under current conditions. Under the +40 years scenario, no beaches would be above the 50 % female ratio when considering July and August together when most turtles could nest (Table 3), but 4 out of the 19 beaches (Palma, Cala Tarida, Portinatx and Ses Salines) would reach slightly above 50 % female in August. Only under the +80 years scenario, 7 beaches could potentially have sex ratios above 60 % female in July and August (Table 3) of which, 4 of these beaches are in Ibiza (Es Cavallet, Portinatx, Ses Salines and Cala Tarida), 2 beaches in Menorca (Sa Mesquida and Cala Tirant) and one beach in Mallorca (Palma).

4. Discussion

Sea turtle population growth is generally driven by the number of nesting females (Hays et al., 2017; Santidrián Tomillo et al., 2021). Because sea turtles have multiple paternity and females can typically mate with several partners and store sperm (Lee et al., 2018), populations could persist with a relatively small number of male turtles, as long as the number of males was enough to fertilize the eggs (Hays et al., 2010). However, rapid and long-lasting warming events could change the drivers of population dynamics if fertility rates declined due to a scarcity of males. Sex ratio theory stands that producing the rare sex in a population is advantageous for parents, as it increases the changes of future reproduction of the offspring (Fisher, 1930; Hamilton, 1967). If males progressively became "the rare sex" under climate change, indicated by a decline in the probability of egg fertilization, we could expect that turtles would adapt behaviorally and physiologically to produce more males. The same holds true for impacts on egg survival. As mortality of embryos during incubation increases due to rising temperatures (Santidrián Tomillo et al., 2014; Booth et al., 2020), turtles could respond by searching for new areas that provide cooler conditions that favor egg development or by nesting during cooler months (Patrício et al., 2021).

While colonization of new nesting beaches could be one strategy of adaptation to increase embryo survival and production of male hatchlings, beaches with male-biased sex ratios may fail to establish long-term nesting populations. Sea turtles are philopatric with most individuals returning to nest to the general area where they emerged as hatchlings, but with some individuals that disperse (Bowen and Karl, 2007; Miller et al., 2003). Thus, new beaches that only or mainly provide male hatchlings could still be critical for sea turtles under climate change, but a nesting population may not be established until the percentage of female hatchlings increases and turtles return to nest. Our projections indicated that the Balearic Islands would mainly provide male hatchlings now and under future conditions (Fig. 6), potentially providing a climate refuge for loggerhead turtles in the short and long term. Because the percentage of female hatchlings is projected to increase throughout the 21st century, especially in nests incubating in July and August (Fig. 6), the establishment of a nesting population could occur toward the end of the century, but only at a few sites. Loggerhead turtles are long-lived and late maturing species (Heppell, 1998; Mayne et al., 2020). Consequently, even if the number of sporadic nests continued increasing and turtles nesting at the Balearic Islands were highly philopatric, the colonization process could still take a long time. While a male-biased sex ratio could potentially limit the speed of the colonization process, a change toward more optimal conditions in water temperature could favor an increase in the number of (1) new turtles colonizing the area and (2) clutches a single female could lay (if having enough reserves to produce more clutches), due to an expansion of the temporal window for nesting. Changes in phenology in relation to climate change have been observed in some temperate areas where turtles arrive earlier to nest in response to warmer conditions (Weishampel et al., 2004; Mazaris et al., 2009). Since the optimal time for loggerhead nesting in the Mediterranean is constrained to the summer months (Schofield et al., 2009, 2021) and possibly more so in western areas (Santidrián Tomillo et al., 2022), a temporal expansion of optimal conditions in the water could contribute to enhance the colonization process.

The beaches of the Balearic Islands could provide a wide range of thermal conditions for loggerhead turtle nests. Spatial variability in thermal conditions among beaches, as well as variability in seasonal and interannual temperatures were similar to those of other nesting sites in the Mediterranean (Zbinden et al., 2007; Katselidis et al., 2012), with temperatures varying by up to several degrees between years, months and beaches. As expected, not all beaches were equally suitable for nesting. Whereas some beaches were projected to have temperatures consistently below the viable range (5 out of 19 beaches under current conditions), others could provide suitable temperatures under current and future conditions, and practically all beaches by the end of the 21st century (Table 3). However, only seven beaches were projected to provide primary sex ratios similar to those currently estimated for most

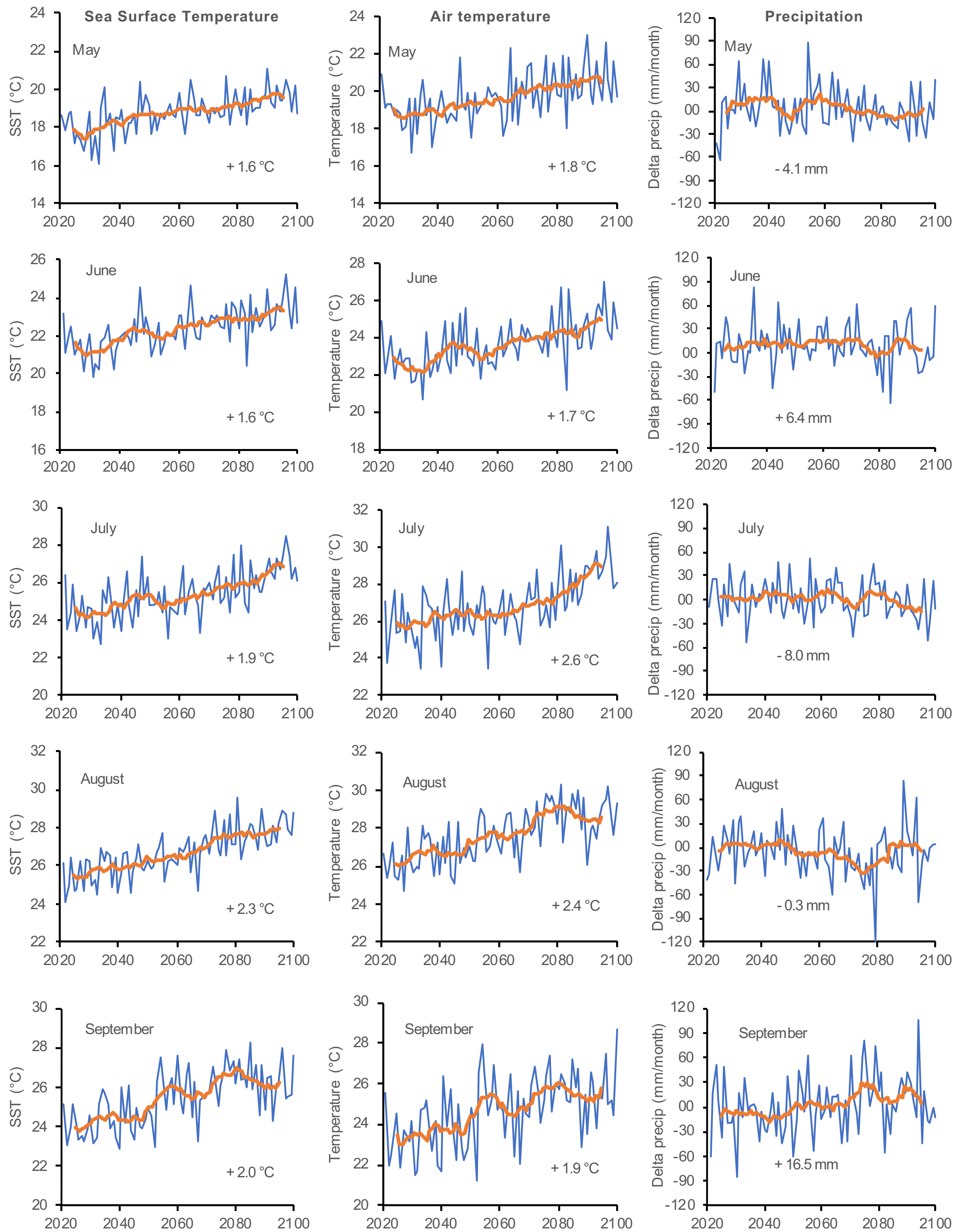

Fig. 4. Climate change projections of Sea Surface Temperature (SST), air temperature (°C) and precipitation (mm) for the Balearic Islands throughout the 21st century from NOAA GFDL's high-resolution global climate model. Air temperature and precipitation are projections for the island of Ibiza. Red line indicates the 10-year moving average. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sea turtle rookeries (~60–80 % female) (reviewed in Hays et al., 2017) by the end of the 21st century (Table 3).

This study has several methodological shortcomings that need to be acknowledged. First, we simulated thermal conditions in the center of a clutch by measuring temperatures at the average depth of a loggerhead nest. Because nests are complex structures, several variables could influence the thermal environment that ultimately affect hatching success and sex ratio (e.g. number of developing embryos, humidity, grain size and depth; Ackerman, 1997, Miller, 1997). In addition, correlative models such as the one that we used here can be good at estimating sand

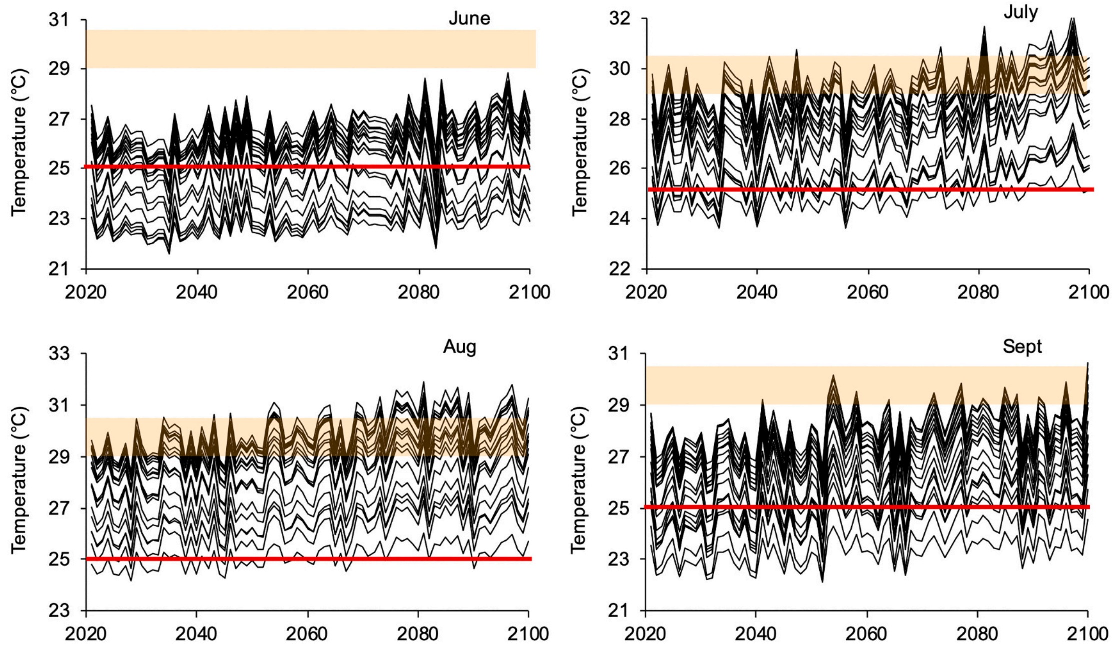

Fig. 5. Mean nest temperature projections for 19 beaches at the Balearic Archipelago throughout the 21st century. Shaded area indicates the transitional range of temperatures over which both sexes of hatchlings are produced. Temperatures below 29.0 °C result in 100 % male hatchlings and above 30.5 °C in 100 % female hatchlings based on Rees and Margaritulis (2004, modified from Mrosovsky et al., 2002). Red line indicates the lower temperature threshold (25 °C) for egg development. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Mean inferred nest temperatures (°C) and sex ratio (female percentage) in July and August under current and climate change scenarios (+40 and + 80 years) for 19 beaches at the Balearic Islands. Beaches are sorted from the highest to the lowest mean nest temperature under current condition. Shaded areas indicate temperatures below the viable range for embryo survival.

		Current conditions		+40 years		+80 years	
Beach	Island	Tmean	Sex ratio July-August	Tmean	Sex ratio July-August	Tmean	Sex ratio July-August
TAR	Ibiza	28.1	33.8%	28.5	45.8%	29.5	84.0%
POR	Ibiza	28.0	12.4%	28.4	32.4%	29.2	68.3%
SAL	Ibiza	27.9	24.1%	28.3	34.2%	29.1	67.3%
CAV	Ibiza	27.8	22.6%	28.1	33.5%	29.1	69.1%
MES	Menorca	27.7	25.6%	28.1	35.9%	29.0	75.2%
PAL	Mallorca	27.4	20.7%	28.1	34.7%	28.9	68.5%
PUJ	Formentera	27.4	6.6%	27.6	13.7%	28.4	39.9%
MIG	Formentera	27.3	9.0%	27.7	17.2%	28.5	46.4%
TIR	Menorca	27.1	15.7%	27.7	33.0%	28.8	73.1%
PAG	Mallorca	26.8	3.4%	27.3	9.3%	28.1	27.2%
ATA	Menorca	26.3	0.7%	26.8	3.2%	27.5	15.3%
ALG	Menorca	26.1	2.3%	26.7	6.9%	27.8	37.3%
CME	Mallorca	25.9	1.4%	26.5	4.4%	27.4	14.5%
SCA	Mallorca	25.3	0.7%	26.0	2.3%	26.9	9.3%
SCO	Mallorca	24.9	0.0%	25.4	0.2%	26.1	1.0%
COV	Mallorca	24.4	0.0%	24.8	0.0%	25.5	0.0%
SAM	Mallorca	24.3	0.0%	24.9	0.0%	25.6	0.3%
BIN	Menorca	24.1	0.0%	24.5	0.0%	25.3	0.4%
SON	Menorca	23.6	0.0%	23.9	0.0%	24.4	0.0%

temperatures if correlations with climatic conditions are strong, but the quality of the predictions depend on the acquisition of long-term data (Bentley et al., 2020). Thus, continuing data collection in the long-term at the Balearic Islands and simulating conditions in the nest environment based on other variables could help improve our projections.

Sea turtles do not necessarily nest on all beaches available in a

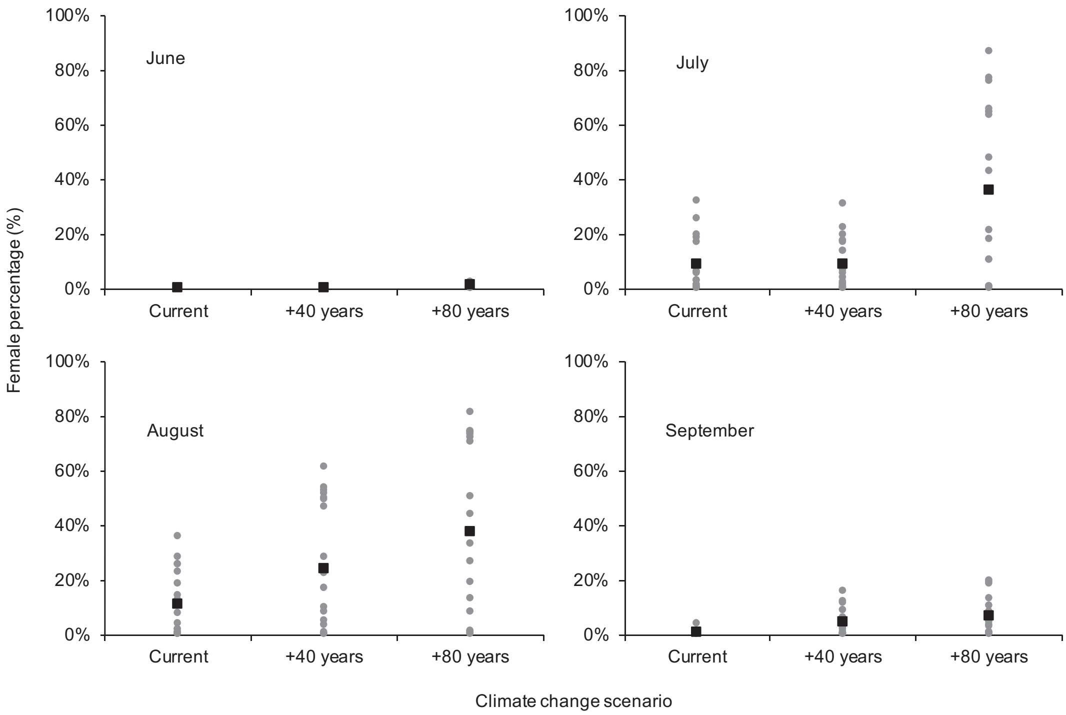

Fig. 6. Projections of mean sex ratios of hatchlings (female percentage) of loggerhead turtles (*Caretta caretta*) at 19 beaches around the Balearic Islands, under current climatic conditions and under climate change scenarios of +40 and + 80 years. Sex ratios are estimated for nests that would have the thermosensitive period for sex determination in June, July, August and September. Each circle represents the mean sex ratio projected for a beach. Mean sex ratio of all beaches is represented with a black square.

particular area, and factors other than climate could influence their nest-site choice. For example, at the island of Zakynthos, Greece, where the largest nesting aggregation for loggerhead turtles in the Mediterranean is found, nesting concentrates within Laganas Bay, in the south eastern part of the island (Mazaris et al., 2006). Among environmental and non-environmental factors that could influence beach choice by sea turtles are beach slope (Wood and Bjorndal, 2000), grain size (Mohd Salleh et al., 2021), risk of erosion or inundation of nests (Eckert, 1987), vegetation patterns (Kamel and Mrosovsky, 2004), predation risk for eggs and hatchlings (Spencer, 2002) and access to currents that would favor the distribution and survival of hatchlings once they entered the water (Maffucci et al., 2016). Therefore, it is possible that not all beaches of good thermal conditions would be chosen by turtles, as there are multiple cues that females could use to select their nesting site. Females could also potentially buffer some negative effects of climate change on nest incubation through spatial or temporal shifts in their nesting distribution (Patrício et al., 2021) or by placing their clutches at different depths (Fuentes and Porter, 2013). Thus, they are able to adjust their behavior to changing conditions.

Finally, coastal development of western Mediterranean beaches is very high, which could complicate the chances of a successful colonization (Hochscheid et al., 2022). Among sea turtle threats associated to coastal development are artificial lights, beach nourishment, human traffic, beach cleaning, predation by domestic animals, pollution, plastic ingestion, boat strikes and fishery bycatch (Lutcavage et al., 1997). The Balearic Islands in particular, are a popular destination for mass tourism (Pons and Rullan, 2014) and the pressure on sea turtle nesting beaches and in the sea could potentially be very high. Plastic ingestion has already been found in many stranded turtles that feed in the Balearic Sea (Solomando et al., 2022) and fishery bycatch around the Balearic Islands could be the most severe in the Mediterranean (Margaritoulis et al., 2003; Casale et al., 2018). On the other hand, some of the studied beaches are located far away from towns and could be dark at night, which could facilitate nesting of adult turtles and sea-finding of emergent hatchlings. These beaches however, are still highly visited during the day, which could threaten nests by compacting sand and with the use of umbrellas that could break eggs or shade nests (Margaritoulis, 1990; Lopez et al., 2015). A high number of recreational boats also anchor near the coasts of the Balearic Islands (Balaguer et al., 2011), which could make an additional threat to any turtles accessing the beaches to nest or resting during the internesting interval.

The peak of tourism coincides with the sea turtle nesting season in the Mediterranean (Schofield et al., 2021; Hochscheid et al., 2022), making protection ultimately dependent on active management. The Balearic Islands could potentially provide good climate refuge for Mediterranean loggerhead turtles, with thermal conditions becoming increasingly optimal both in land and sea. However, as climate gets warmer, it will be necessary to actively reduce other ongoing anthropogenic threats to facilitate the adaptation of sea turtle populations to the new climatic conditions.

CRediT authorship contribution statement

PST, JT and AM conceived the study. AM provided data on sand temperatures previously collected for the Balearic Archipelago. FP, GF and VNR contributed to the data collection. VS provided projections of climatic conditions under climate change scenarios. PST analyzed data and wrote the manuscript with input from all authors.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

The data will be provided on reasonable request

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110146.

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