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Contribution to the Theme Section 'Species range shifts, biological invasions and ocean warming'

Environmental changes in the Mediterranean Sea could facilitate the western expansion of loggerhead turtles

P. Santidrián Tomillo[1,*], J. Tomás[2], A. Marco[3], A. Panagopoulou[4], G. Tavecchia[1]

[1]Animal Demography and Ecology Unit, GEDA, Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Miquèl Marques 21, 01790 Esporles, Spain
[2]Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, Catedrático José Beltrán 2, 46980 Paterna, Valencia, Spain
[3]Estación Biológica de Doñana, CSIC, C/ Américo Vespucio, S/n, 41092 Sevilla, Spain
[4]ARCHELON, The Sea Turtle Protection Society of Greece, 10432 Athens, Greece

ABSTRACT: Climate change may affect life on Earth in multiple ways. Whereas some populations may encounter detrimental conditions that cause extirpations, those occupying cooler thermal limits of a range may benefit by expanding. For sea turtles, egg maturation in the female oviduct and nest incubation are temperature-dependent and vulnerable to climate change. Mediterranean loggerhead turtles *Caretta caretta* nest in the eastern basin although sporadic nesting occurs on the western side. To assess the likelihood of a climate-related expansion, we compared historical air and sea surface (SST) temperatures between locations near established eastern nesting areas and western areas where sporadic nesting is increasing (Palinuro, Italy) or just started (Balearic Islands, Spain). Our results suggest that summer air and water temperatures in western sites were suitable for nesting over the last 40–50 yr, at least in July–August, having (1) SSTs above suboptimal threshold temperature (22°C) and (2) similar air temperatures to those of Greece, but among the lowest in the Mediterranean. There was a decreasing east-to-west gradient in SST. However, SSTs were similar around beaches of Zakynthos (Greece), Palinuro and Ibiza (Balearic Islands), where SST was above 22°C for at least 60 d, potentially allowing turtles to lay multiple clutches. A warming trend was detected in air temperature and SST since the 1970s–1980s. Although conditions in the western Mediterranean currently seem suitable for nesting, lower air temperatures in May–June and higher precipitation in September could shrink the nesting window. If warming continues, conditions in the western basin could progressively become more favorable for nesting.

KEY WORDS: Mediterranean · Climate change · Sea turtle · Loggerhead · *Caretta caretta* · Sea surface temperature · SST · Temperature · Colonization

1. INTRODUCTION

Animal distributions could be widely impacted by climate change (Anderson 2013, Pecl et al. 2017). In Europe, for example, species richness of terrestrial mammals is expected to decline in the warmer Mediterranean region, but increase at the cooler northern latitudes due to the shift of many species' distributions (Levinsky et al. 2007). This phenomenon is particularly evident in the marine environment, where the distribution of species can shift faster than in terrestrial environments in relation to changes in water

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[*]Corresponding author: psantidrian@imedea.uib-csic.es

[§]Advance View was available November 3, 2022 temperature, possibly because dispersal is easier and thermal margins are narrower (Poloczanska et al. 2013, Lenoir et al. 2020).

Sea turtles are highly philopatric, with most adult turtles returning to their general area of origin to nest (Bowen & Karl 2007, Stiebens et al. 2013), where eggs can incubate on suitable nesting beaches. Although most turtles exhibit natal-homing behavior, some individuals move over long distances to breed (Miller et al. 2003, Bowen & Karl 2007). The variability in nesting strategies may allow sea turtles to adapt to stochastic environmental changes through colonization of new nesting areas. Contrary to other species, the establishment of new nesting colonies, if successful, could take several decades considering that most individuals exhibit a high level of philopatry (Bowen & Karl 2007) and that sea turtles are long-lived and late-maturing (loggerhead turtles *Caretta caretta* live ~up to 60 yr and reach maturity in ~20–35 yr; Heppell 1998, Mayne et al. 2020).

Genetic studies have facilitated the detection and timing of sea turtle colonization worldwide (Bowen & Karl 2007). The colonization of the Mediterranean Sea by loggerhead turtles may have occurred in several waves (Clusa et al. 2013, Baltazar-Soares et al. 2020), the most recent one being after the last glaciation retreated ~11 700 yr ago (Carreras et al. 2018, Baltazar-Soares et al. 2020). In the last 2–3 decades, increasing numbers of sporadic nesting in the western Mediterranean has prompted researchers to hypothesize whether new colonization events could be underway, possibly in relation to climate warming (Maffucci et al. 2016, Carreras et al. 2018). However, an expansion in the nesting distribution of loggerhead turtles in the Mediterranean could also result from the increasing trend in nesting numbers in the eastern basin (Casale et al. 2018 and references therein).

Several conditions at sea and on the shore need to occur simultaneously for a colonization attempt to become successful: (1) turtles need to encounter optimal water temperatures for egg maturation in the female oviduct (typically ≥22°C, Hays et al. 2002, Schofield et al. 2009, 2021) and (2) nesting beaches must provide suitable thermal conditions within viable ranges for egg development (~25–35°C) over the duration of the incubation period (Ackerman 1997). In addition, females must encounter males in the new area to fertilize the eggs or store sperm from past encounters (Schofield et al. 2017). Anthropogenic (e.g. artificial lights) and natural threats (e.g. erosion, predation) to clutches and hatchlings must also be sufficiently low (Salmon 2006, Leighton et al. 2011), and dispersal conditions for hatchlings after entering the water must favor their survival (Maffucci et al. 2016). Loggerhead turtle nests have been recorded in the western Mediterranean since 2001 (Tomás et al. 2002), producing viable hatchlings (Tomás et al. 2008, Carreras et al. 2018, González-Paredes et al. 2021). This indicates that eggs were fertilized and beaches provided suitable thermal conditions for egg development. If these beaches were colder than eastern Mediterranean beaches, the hatchling sex ratio could be male-biased because sea turtles have temperature-dependent sex determination and males are produced at low temperatures (Standora & Spotila 1985). In Mediterranean loggerhead turtles, mean temperatures below 29°C during the middle third of incubation produce ~100% male hatchlings, and above 30.5°C they produce ~100% female hatchlings, with mixed sexes being produced in between (Rees & Margaritoulis 2004, based on Mrosovsky et al. 2002).

Water temperature is vital to the successful reproduction of sea turtles because the occurrence of egg maturation in the female oviduct and the rate of development are temperature-dependent (Hays et al. 2002, Schofield et al. 2009). As a result, water temperature allows nesting at particular sites, affects when it happens (Weishampel et al. 2004) and determines the duration of the internesting period (Hays et al. 2002, Weber et al. 2011). Essentially, the warmer the water is, the shorter the inter-nesting period becomes because of faster developmental rates (Sato et al. 1998, Valverde-Cantillo et al. 2019), and the earlier the onset of the nesting season occurs (Weishampel et al. 2004). Although loggerhead turtles nest at higher latitudes than other sea turtles (Dodd 1988, Hawkes et al. 2007a) and can inhabit waters below 15°C in the western Mediterranean during the winter (Hochscheid et al. 2005), they still need to encounter warm temperatures in the weeks before and during the nesting season to reproduce (Schofield et al. 2021).

Typical water temperatures around sea turtle nesting beaches are between 25 and 30°C (Hays et al. 2002, Blanco et al. 2013, Hill et al. 2017, Valverde-Cantillo et al. 2019), but turtles during the internesting period could encounter temperatures as low as 22°C (Hays et al. 2002) or above 30°C (Storch et al. 2005) in some areas. In Greece, where the water takes some time to warm up in the summer, loggerhead turtles may encounter similar temperatures in the peak of the summer but much cooler temperatures at the beginning of the nesting season, narrowing the optimal time for nesting and conditioning the number of clutches turtles can lay (Schofield et al.

2009, 2021). Loggerhead nesting in Greece occurs when mean water temperatures are above 22°C and conditions are optimal when temperatures are between 26 and 29°C (Schofield et al. 2009, 2021).

The number of sporadic loggerhead turtle nests in the western Mediterranean has increased in the last 2 decades and particularly, along the Italian and Spanish coasts (Maffucci et al. 2016, Carreras et al. 2018). Along the Campanian region, in southwest Italy, where the number of nests is recorded annually, the number of sporadic events has increased from 1 nest every 2–4 yr in the first years of the 21st century to 1–7 nests per year between 2012 and 2015 (Maffucci et al. 2016).

Due to the increase in the number of sporadic loggerhead nests in the western Mediterranean in recent years, our objective was to assess the suitability of terrestrial and marine environmental conditions for successful nesting through a comparative approach. In particular, we analyzed the suitability of the Archipelago of the Balearic Islands in Spain and Palinuro, Italy, as nesting grounds for loggerhead turtles, by comparing precipitation and air and water temperatures on and around these sites to those of the most important nesting areas in the Mediterranean in the second part of the 20th century. The beginning of sporadic nesting occurred approximately 20 yr later at the Balearic Islands (first reported in 2019) than at Palinuro (nesting started at the beginning of the 21st century). We compared oceanic thermal conditions since 1854 around the areas where nests have been recorded in Spain and in Italy in the last 2 decades, to those around the main nesting beaches in the eastern Mediterranean. Understanding historical and current differences in climatic conditions between established nesting populations and sites where sporadic nesting occurs and is increasing will help us pinpoint the conditions that foster successful colonization events.

2. MATERIALS AND METHODS

2.1. Sea surface temperature

We used 2 different approaches to analyze sea surface temperature (SST). As a first approach, we used monthly SST data with a resolution of 2° × 2° (latitude × longitude) that allowed us to compare general patterns among selected sites across the Mediterranean over ~170 yr. As a second approach, we obtained SST data at a finer resolution (0.25° × 0.25°) in the vicinity of some of the known nesting beaches. This second dataset provided daily SST data covering a small area around the nesting beaches and was available since 1981.

2.1.1. SST at 2° × 2°

We obtained monthly SST from the Extended Reconstructed Sea Surface Temperature (ERSST) v5 from the National Centers for Environmental Information (NCEI) of the National Oceanic and Atmospheric Administration (NOAA) of the USA (https://www.ncei.noaa.gov/products/extended-reconstructed-sst). This dataset is derived from the International Comprehensive Ocean-Atmosphere Dataset (ICOADS) and has a resolution of 2° × 2° (latitude × longitude). This resolution allowed us to go back over one and a half centuries (from 1854 to 2020). We obtained SST for 7 selected areas across the Mediterranean. Five of these areas were located on the eastern side and comprised the main loggerhead nesting beaches in the Mediterranean (2° × 2° areas) around (1) Zakynthos and Kyparissia, Greece, (2) Crete, (3) Turkey, (4) Cyprus and (5) Sirte, Libya. The other 2 areas were located in the western Mediterranean, near the coasts of Spain and Italy (Fig. 1). We used SST for the winter (December–February), spring (March–May), summer (June–August) and fall (September–November) and by month. We used 10 yr moving averages for visual representation of temperature data.

2.1.2. SST at 0.25° × 0.25°

To conduct a finer analysis of the conditions that would affect loggerhead turtles while they are in the vicinity of the nesting beaches, we obtained Optimum Interpolation SST version 2.1 derived from the Advanced Very High Resolution Radiometer (AVHRR) from NCEI, NOAA (https://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst21Agg.html). We obtained daily SST for years between 1981 and 2020. For this analysis, we selected 3 areas: (1) a 0.25° area around Zakynthos, Greece, where the movements of loggerhead turtles have been studied in relation to SST (Schofield et al. 2009, 2021), (2) the area around Ibiza, Spain, where loggerhead nests have only been recently recorded and (3) the area around Palinuro, Italy, where most nests have concentrated in the western Mediterranean (based on Maffucci et al. 2016) (Fig. 1).

To assess the suitability of water temperatures to allow egg maturation in the female oviduct, we used

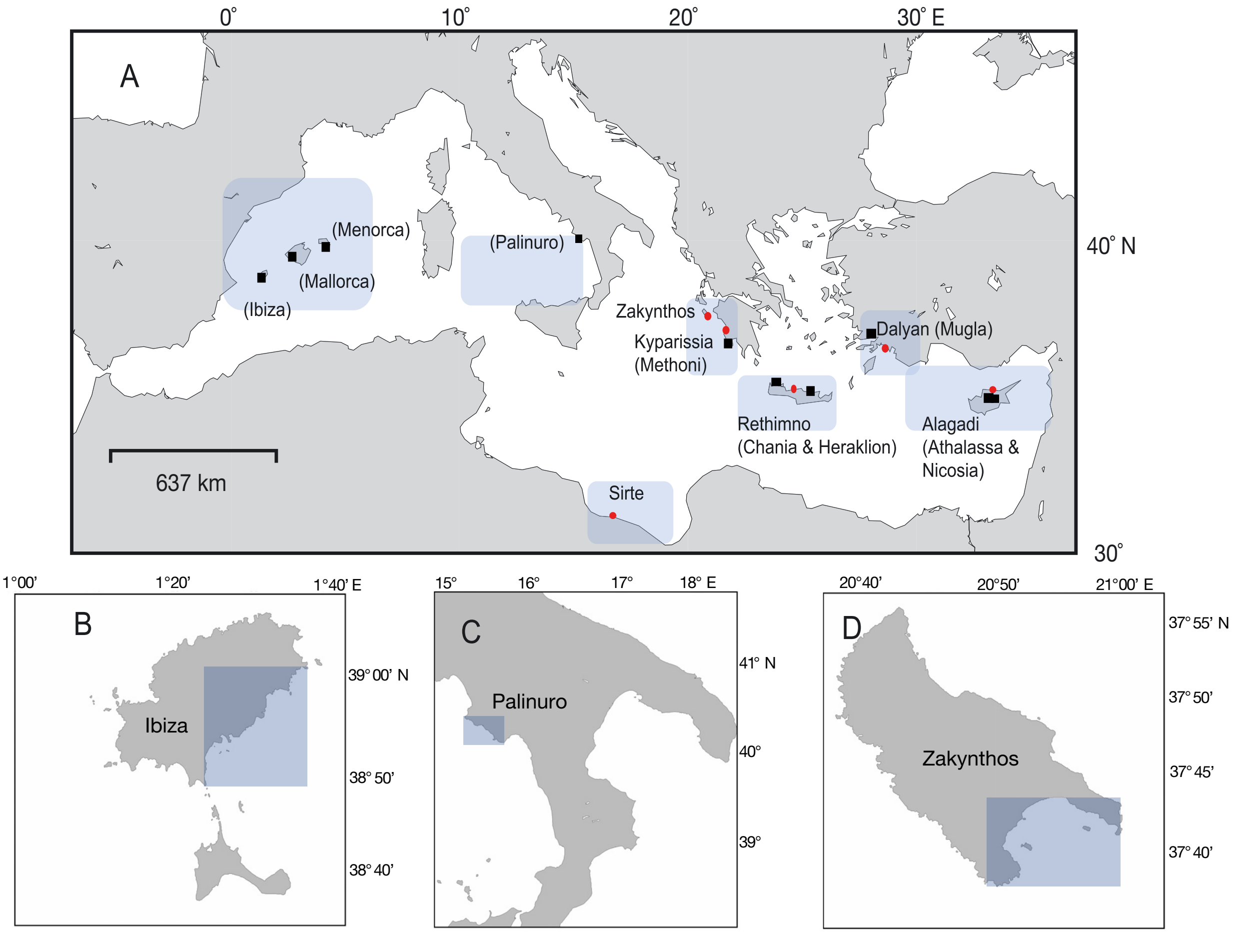

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Fig. 1. (A) Main loggerhead nesting beaches in the Mediterranean (red circles): Zakynthos, Kyparissia and Rethimno, Greece; Dalyan, Turkey; Alagadi, Cyprus; and Sirte, Libya. Also shown are locations of nearby weather stations (black squares; names in brackets) and areas considered for the sea surface temperature (SST, °C) 2° × 2° (latitude × longitude) analysis (blue). The 7 SST areas included 2 locations in the western Mediterranean (Italy and Spain) as well as 5 areas around the main nesting beaches in the eastern Mediterranean (Zakynthos and Kyparissia, Crete, Turkey, Cyprus, and Sirte). (B–D) SST areas in the vicinity of the nesting beaches of Ibiza, Palinuro and Zakynthos, respectively, used in the 0.25° × 0.25° (latitude × longitude) analysis

2 temperature thresholds: 22°C as the suboptimal threshold temperature and 26°C as the optimal one (based on Hays et al. 2002 and Schofield et al. 2009, 2021). Since turtles need to encounter suitable water temperatures over at least the duration of an internesting period (~20 d at 22°C, Schofield et al. 2009), we calculated for each study site (1) the date when SST surpassed both temperature thresholds and (2) the number of consecutive days on which SST was above each temperature threshold. We excluded September from this calculation, as water temperatures could still be high to allow nesting at this time, but nest temperatures can drastically decline in September due to rainy and overcast conditions (Rees & Margaritoulis 2004). We compared SST between sites and assessed the occurrence of changes between 1981 and 2020.

2.2. Air temperature and precipitation

Because nest temperatures are in general highly correlated to air temperatures (Laloë et al. 2021a), we used air temperatures as a proxy of thermal conditions for egg incubation in the study areas. Long-term climatic data are often available from weather stations located at airports around the world. We obtained local climate data from weather stations that were freely available from NCEI, NOAA (https://www.ncdc.noaa.gov/cdo-web/).

Previous studies on the effect of local climate on sea turtle nests around the world have used data from weather stations that were located at distances of ~50 km (Santidrián Tomillo et al. 2012), between 34 and 215 km (Montero et al. 2019) and 150 km (Laloë et al. 2021b). We selected 10 weather stations that were located at a maximum distance of 60 km from nesting sites (Table 1). We obtained monthly maximum, minimum and mean air temperatures (°C) from each weather station. Although rainfall during the nesting season (summer) is minimal in the Mediterranean, we obtained information on monthly precipitation (mm) to analyze if there were differences among sites. Seven of the stations were located near well-known loggerhead turtle nesting beaches in the eastern Mediterranean and the other 4 were located on the western side, where nesting has been typically low and sporadic. Among the latter, 1 station was located at Cape Palinuro, Italy, where the number of sporadic nests seems to be increasing (Maffucci et al. 2016) and the other 3 stations were located at the Balearic Islands (Mallorca, Menorca and Ibiza), where sporadic nesting has only been recently documented (Table 1, Fig. 1).

Specifically, weather stations in the eastern Mediterranean were located at Methoni (near Kyparissia beach, Greece, 48 km), Heraklion and Chania, Crete, Greece (both located near Rethimno beach, 60 and 46 km, respectively); Mugla, Turkey (52 km from Dalyan nesting beach); and Athalassa and Nicosia, Cyprus (both at 22 km from Alagadi nesting beach) (Table 1, Fig. 1). Within the Balearic Islands , the stations were located at Menorca and Ibiza (7 and 2 km, respectively, from beaches where loggerhead turtles nested in 2019 and 2020) and at Mallorca (Palma de Mallorca city port where no nests have yet been recorded). To simplify the analysis, we only used data from Ibiza for the inter-Mediterranean site comparisons because Ibiza and Mallorca had similar climatic conditions ($p > 0.05$ in pairwise Wilcoxon post hoc tests for all months; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m728p145_supp.pdf) and more nests had been placed in Ibiza than in Menorca. For all stations, we considered data for the period between May and September (both included) when nests have been recorded in the Mediterranean. We included information for all available years between 1950 and 2020, but time periods varied among sites (Table 1).

We used a Shapiro-Wilk test to assess for normality in the temperature datasets. Since data were not normally distributed, we used a Kruskal-Wallis test to compare temperatures between sites, followed by a pairwise Wilcoxon post hoc test (Bonferroni adjusted) to determine where any differences could be. We also used a Mann-Kendall test to detect time-series trends. All statistical analyses were done in R (version 4.1.2) (https://www.r-project.org).

3. RESULTS

3.1. SST at 2° × 2°

Between 1854 and 2020, there have been several periods with cooling and warming trends in SST throughout the Mediterranean. Periods of warming occurred in 1850–1870, 1910–1950 and 1975–2020 (Fig. 2), and the most recent one may still be ongoing. Peaks in SST in the Mediterranean occurred around 1870, 1950 and 2020, with SSTs currently being the warmest they have been since the 1850s, but closely followed by SSTs around 1870 and 1950 (Fig. 2). In Spain, for instance, there was an overall increase of ~0.5°C across all seasons over the 166 yr. Since the 1970s, SST has increased by ~1.0°C in the spring and over 1.5°C in the summer (Fig. 2).

Although the trends in SST were very similar across the Mediterranean, there were marked differences among sites with a decreasing east to west gradient in water temperature (spring: $\chi^2 = 910.5$, df = 6, $p < 0.001$; summer: $\chi^2 = 668.7$, df = 6, $p < 0.001$; fall: $\chi^2 = 920.0$, df = 6, $p < 0.001$ and winter: $\chi^2 = 996.12$, df = 6, $p < 0.001$) (Fig. 2; Fig. S2). Water temperatures were warmest in Cyprus for any time of the year, followed by Sirte (~1.0°C cooler than Cyprus), Turkey and Greece (~1.5–2.0°C cooler than Cyprus), Italy (~3.0°C cooler than Cyprus) and Spain (~3.5°C cooler

Table 1. Location of weather stations included in the study and corresponding nearest loggerhead nesting beaches, distance between the weather station and the nesting beach and range of years over which air temperatures (°C) were available. Concerning the Balearic Islands, nesting in Menorca and Ibiza was sporadic, and no nests have been recorded in Mallorca to date. Data range for Palinuro (Italy) was incomplete

Weather station	Nearest nesting beach	Country	Distance (km)	Year range
Mallorca	–	Spain	–	1973–2019
Menorca	Punta Prima	Spain	7	1970–2019
Ibiza	Platja d'en Bossa	Spain	2	1970–2019
Palinuro	Palinuro	Italy	4	1966–2019 (incomplete)
Methoni	Kyparissia	Greece	48	1956–2011
Heraklion	Rethimno	Greece	60	1955–2004
Chania	Rethimno	Greece	46	1961–2004
Mugla	Dalyan	Turkey	52	1966–2020
Athalassa	Alagadi	Cyprus	22	1983–2013
Nicosia	Alagadi	Cyprus	22	1971–2000

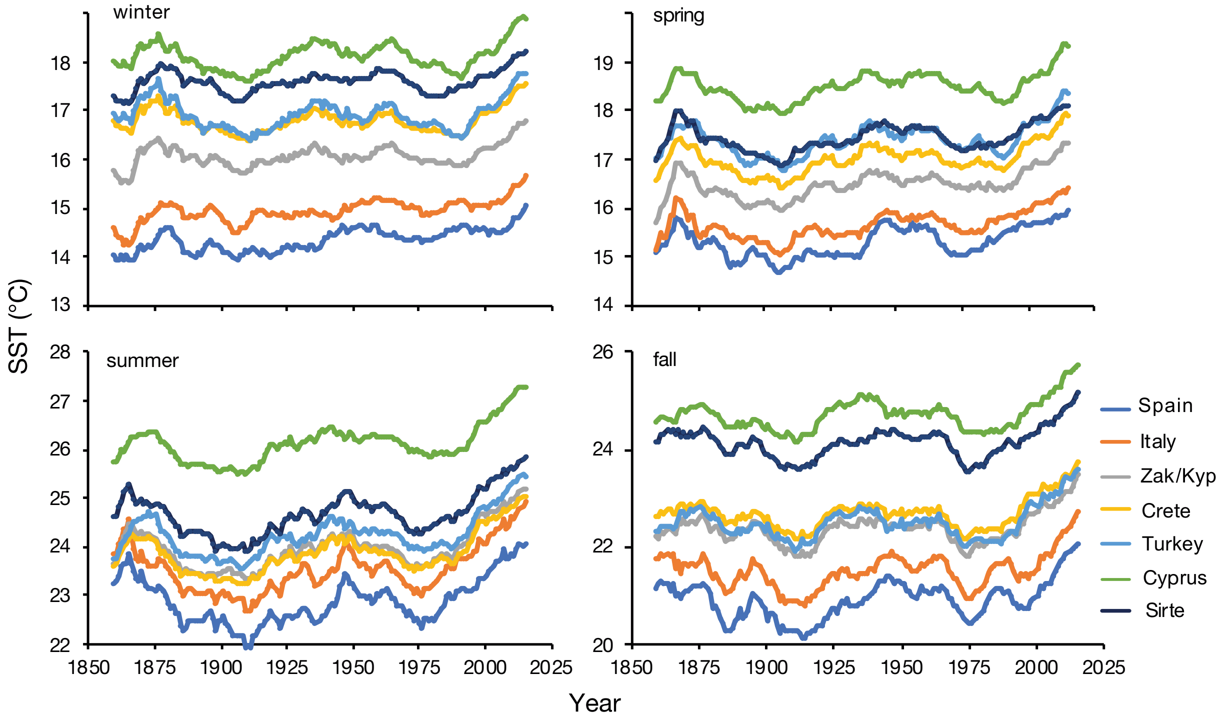

Fig. 2. Mean sea surface temperature (SST, °C) recorded in areas encompassing the main nesting beaches for loggerhead turtles in the Mediterranean (Zakynthos/Kyparissiaand Crete, Greece; Turkey; Cyprus; and Sirte, Libya) and for areas encompassing recent nesting sites (Italy, Spain) per quarter of the year between 1855 and 2020. Quarters of the year correspond to winter (December–February), spring (March–May), summer (June–August) and fall (September–November) in the northern hemisphere. Data are represented as 10 yr moving averages

than Cyprus) (Fig. 2; Fig. S2). Although water temperatures in Italy were at least 1°C lower than in Turkey and Greece in the fall, winter and spring, they were similar in the summer, especially in recent years. SST in Spain was consistently lower than that at the other sites during all seasons and all years ($p < 0.001$ in all cases), but with smaller differences in the summer (Table 2).

In the comparison of mean monthly SST from May to August between the western Mediterranean sites (Spain and Italy) and Zakynthos/Kyparissia, where the effect of SST on loggerhead turtle nesting has been studied, we found that (1) water temperature in May was below the 22°C threshold at all sites (Fig. 3), (2) SST in June was only above the 22°C threshold in Zakynthos/Kyparissia over the years comprising the 3 warming periods, as well as in Italy around 1870 and after the 1990s–2000s and (3) mean monthly temperatures were above the 22°C threshold in July and August at the 3 sites (Fig. 3).

Table 2. Mean ± SD difference in sea surface temperature (°C) between Spain, where sporadic nesting of loggerhead turtles has been recorded; Italy, where nesting is also sporadic but at greater numbers; and areas of established nesting rookeries: Zakynthos/Kyparissia (Zak/Kyp) (Greece), Crete (Greece), Turkey, Cyprus and Sirte (Libya) for the time period 1855–2020. All comparisons were significantly different at $p < 0.001$

	Italy–Spain	Zak/Kyp–Spain	Crete–Spain	Turkey–Spain	Cyprus–Spain	Sirte–Spain
Winter	0.6 ± 0.3	1.7 ± 0.6	2.4 ± 0.7	2.6 ± 0.8	3.8 ± 0.7	3.2 ± 0.4
Spring	0.4 ± 0.3	1.2 ± 0.5	1.7 ± 0.6	2.1 ± 0.7	3.2 ± 0.6	2.1 ± 0.4
Summer	0.6 ± 0.3	1.1 ± 0.6	1.0 ± 0.7	1.3 ± 0.8	3.2 ± 0.7	1.8 ± 0.5
Fall	0.6 ± 0.4	1.5 ± 0.7	1.8 ± 0.8	1.6 ± 0.9	3.8 ± 0.8	3.2 ± 0.5*
May	0.4 ± 0.5	1.3 ± 0.8	1.7 ± 0.9	2.2 ± 1.1	3.5 ± 1.0	1.9 ± 0.6
June	0.7 ± 0.5	1.5 ± 0.9	1.6 ± 1.1	2.1 ± 1.2	3.5 ± 1.1	1.8 ± 0.6
July	0.7 ± 0.4	1.0 ± 0.8	0.9 ± 0.9	1.2 ± 1.0	3.2 ± 0.9	1.7 ± 0.6
August	0.6 ± 0.4	0.7 ± 0.8	0.5 ± 1.0	0.7 ± 1.1	3.0 ± 1.0	1.9 ± 0.6
Annual	0.6 ± 0.2	1.4 ± 0.4	1.7 ± 0.4	1.9 ± 0.5	3.5 ± 0.4	2.6 ± 0.3

3.2. SST at 0.25° × 0.25°

The SST analysis that focused on the vicinity of the nesting beaches yielded slightly different results. SST was statistically significantly lower than in Zakynthos ($p < 0.001$ in May and June) only early in the summer and for Ibiza. In general, there were statistically significant differences in SST between the 3 sites for all months ($p < 0.01$ all cases), but the warmest and coolest sites were not always the same. Unlike in the 2° × 2° analysis, we found that SST was not always warmer in Zakynthos than at the other 2 sites. In fact, the warmest temperatures were recorded in Palinuro in most months (June, July and August, with no statistical differences between Palinuro and Zakynthos in May; $p = 0.17$), and were only warmer in Zakyn-

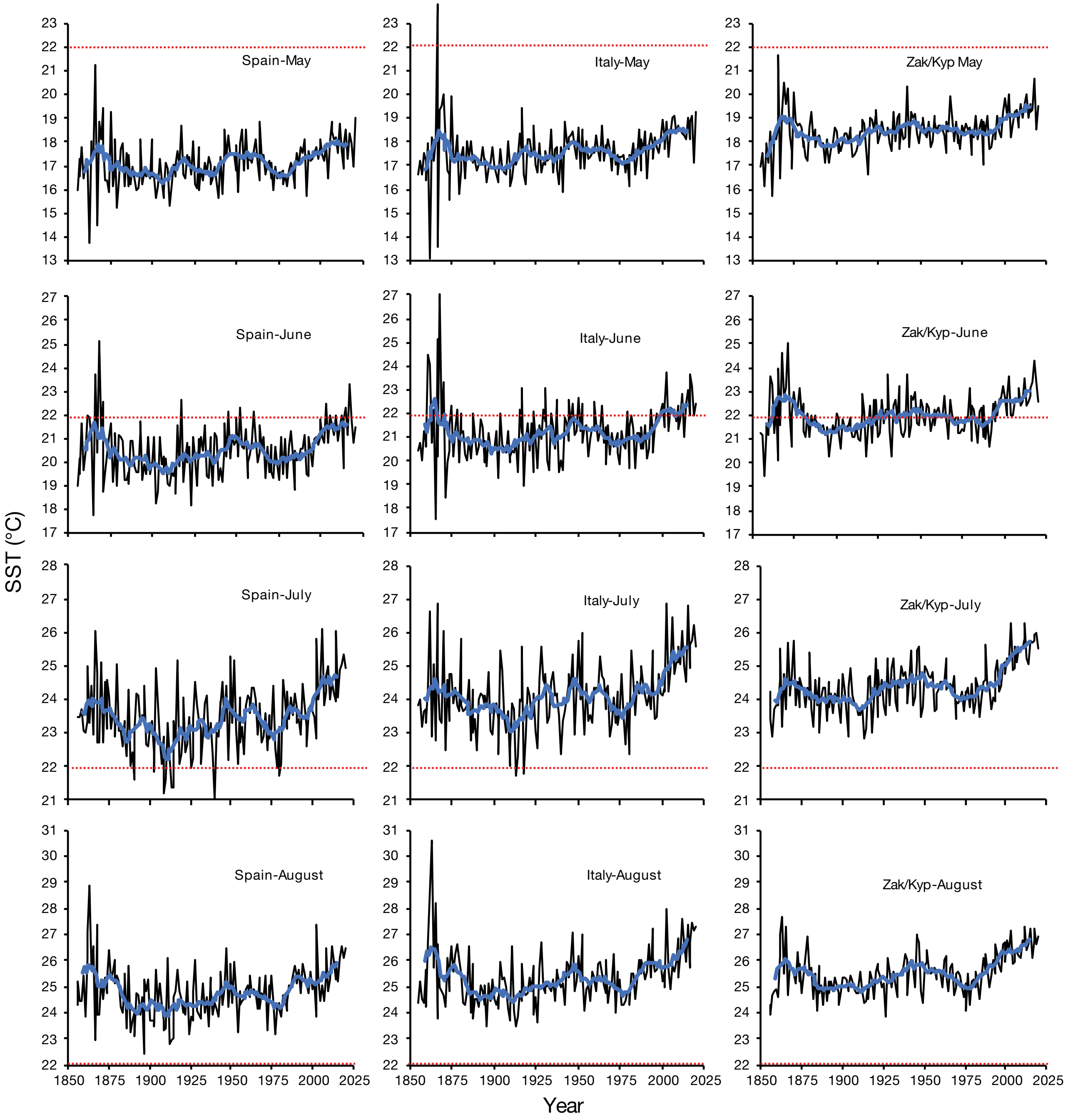

Fig. 3. Mean sea surface temperature (SST, °C) recorded in Spain, Italy and Zakynthos/Kyparissia (Greece) between 1855 and 2020 in May, June, July, August and September. Solid blue line shows 10 yr moving averages. Red dotted line indicates the suboptimal threshold temperature (22°C)

thos than in Palinuro in September. The lowest temperatures were recorded in Ibiza in May and June, in Zakynthos in July and August and in Palinuro in September (Table 3). There were statistically significant differences in SST between all pairs of sites in June, July and August ($p < 0.05$ all cases), but not between Zakynthos and Palinuro in May ($p = 0.17$) or Ibiza and Zakynthos in September ($p = 0.28$). Mean water temperatures were below the 22°C threshold in May at all sites but were above it in all other months.

On the other hand, the date when SST surpassed the 22°C threshold occurred earlier at Zakynthos (mean 11 June) than at Palinuro (mean 16 June) and Ibiza (mean 19 June), with statistically significant differences only detected between Zakynthos and Ibiza ($p < 0.001$). However, the date when SST surpassed the 26°C optimal threshold was not statistically significantly different between sites ($p > 0.05$ all cases), occurring at the end of July in all cases (Table 3). SSTs in the vicinity of the nesting beaches were also above the 22°C threshold for longer than 60 d at all sites (Table 3). This could possibly allow turtles to lay at least 3 clutches during a nesting season (considering an internesting period of ~20 d at 22°C) if they started nesting early. The maximum number of consecutive days with water temperatures above 26°C was comparatively much smaller, with approximately 14 d in Zakynthos and Ibiza and 19.5 d in Palinuro (Table 3). Differences between sites were not statistically significant ($p > 0.05$ all sites).

Over the 40 yr study period, there was a trend toward surpassing the 22 and 26°C thresholds earlier in the season at all sites (both $p < 0.005$) and toward increasing the maximum number of consecutive days above 22 and 26°C (both $p < 0.001$; Fig. 4). The number of consecutive days with water temperatures above 22°C increased from 1981 to 2020 by 13 d in Ibiza and Zakynthos and 10 d in Palinuro. The number of days above 26°C increased by 12 d in Ibiza, 14 d in Zakynthos and 5 d in Palinuro (Fig. 4). This change toward warmer conditions over the 40 yr period could potentially allow turtles to increase the number of clutches (number of days above 22°C extended to ~75 d in Ibiza and ~80 d in Palinuro and Zakynthos) if conditions on land also allowed egg incubation.

Table 3. Mean ± SD sea surface temperature (SST, °C) during the months loggerhead turtles could be nesting, dates when SST surpassed the 22 and 26°C temperature thresholds and the mean (±SD) maximum number of consecutive days (between May and August) on which SST was above the threshold temperatures in the vicinity of nesting beaches at Ibiza (Spain), Palinuro (Italy) and Zakynthos (Greece)

	Ibiza	Palinuro	Zakynthos
SST in May	18.0 ± 1.3	18.7 ± 1.6	18.8 ± 1.4
SST in June	21.4 ± 1.6	22.5 ± 1.7	22.2 ± 1.5
SST in July	24.6 ± 1.2	25.4 ± 1.2	24.5 ± 1.3
SST in August	26.0 ± 0.9	26.5 ± 1.0	25.8 ± 1.0
SST in September	24.8 ± 1.2	24.6 ± 1.2	24.9 ± 1.1
Mean date temperature surpassed 22°C	19 June	16 June	11 June
Mean date temperature surpassed 26°C	29 July	25 July	27 July
Number consecutive days >22°C	67.9 ± 9.7	76 ± 8.9	71.9 ± 12.5
Number consecutive days >26°C	14.1 ± 12.5	19.5 ± 17.0	13.7 ± 14.2

3.3. Air temperatures

A warming trend occurred at most sites and was especially apparent during the summer months. A Mann-Kendall test revealed a positive warming trend in mean air temperatures at 9 out of the 10 sites in June (except Heraklion, $p = 0.30981$), 9 out of the 10 sites in July (except Palinuro, $p = 0.11474$) and 8 out of the 10 sites in August (except Heraklion, $p = 0.23385$, and Methoni, $p = 0.11877$). In May, a warming trend in mean air temperatures was detected at 4 sites (Mallorca, Menorca, Ibiza and Mugla; $p < 0.05$) and in September, at 5 sites (Mallorca, Heraklion, Chania, Mugla and Athalassa; $p < 0.05$). However, there was some variability in the times at which the warming trend occurred (Fig. 5).

The warmest temperatures were recorded at the easternmost sites (Athalassa and Nicosia, Cyprus), and the lowest temperatures in Menorca, Spain (Fig. S3). Comparatively, there were greater differences in air temperature between eastern and western sites at the beginning of the season (May–June) than at the end (July–September) (Table 4). Although temperatures from the western basin stations (Mallorca, Menorca, Ibiza and Palinuro) were in general among the lowest, these were in some months similar or even warmer than temperatures recorded in Greece and Turkey where nesting populations of loggerhead turtles are well established (Fig. S3). For instance, mean temperatures in Ibiza were similar to those of Methoni in May and June (both $p = 1.00$), Turkey in June ($p = 0.080$), Heraklion in July ($p = 1.00$) and Chania in August and September ($p = 1.00$ in both cases), and were warmer than Methoni from July to September ($p < 0.05$) and warmer than Heraklion in August and September ($p < 0.05$ both cases) (Table 4, Fig. 5; Table S1, Fig. S3).

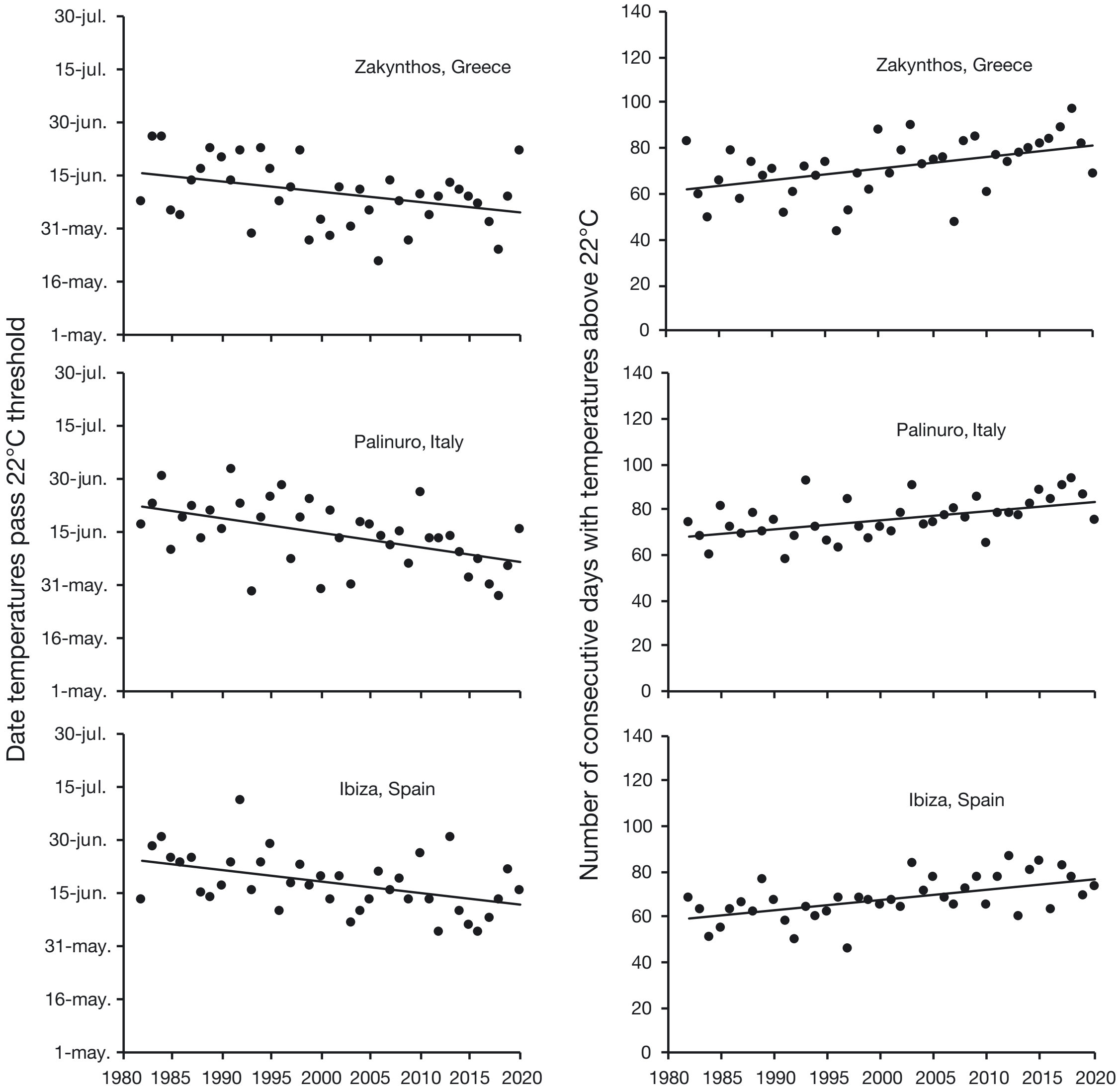

Fig. 4. Date when sea surface temperatures (SST, °C) passed the 22°C suboptimal threshold between 1981 and 2020 and the number of consecutive days SST was above the 22°C threshold at Zakynthos (Greece), Palinuro (Italy) and Ibiza (Balearic Islands, Spain)

Within the Balearic Islands, air temperatures were lower in Menorca than at Mallorca and Ibiza in all months ($p < 0.05$ for all cases), whereas air temperatures in Mallorca and Ibiza were similar to each other in all months ($p > 0.05$ for all cases) (Figs. S1 & S3).

Air temperatures in September were similar to those in June at most sites (Fig. S3), which could allow for successful incubation of eggs during this time. However, mean temperatures in May were below 20°C at all sites, except in Cyprus (Fig. 5).

3.4. Precipitation

Precipitation accumulated during the summer months (June–August) was low, as is characteristic of Mediterranean climate, with mean values below 40 mm at all sites (Fig. 6). Mean precipitation in September was higher at the western sites than anywhere else (mean ± SD: 65.8 ± 72.6 mm in Ibiza and 90.4 ± 60.1 mm in Palinuro) and was highly variable among years (Fig. 6). Differences in the precipitation accumulated in September were statistically significant between the western sites and Crete, Nicosia and Mugla ($p < 0.05$), but not with Methoni ($p = 1.000$, Ibiza–Methoni), although differences between Palinuro and Methoni were marginally significant ($p = 0.0532$). Comparing Methoni to the western sites in other months, statistically significant differences were only found between Methoni and Ibiza in August ($p < 0.01$), with more rain being recorded in Ibiza, and between Methoni and Palinuro in June

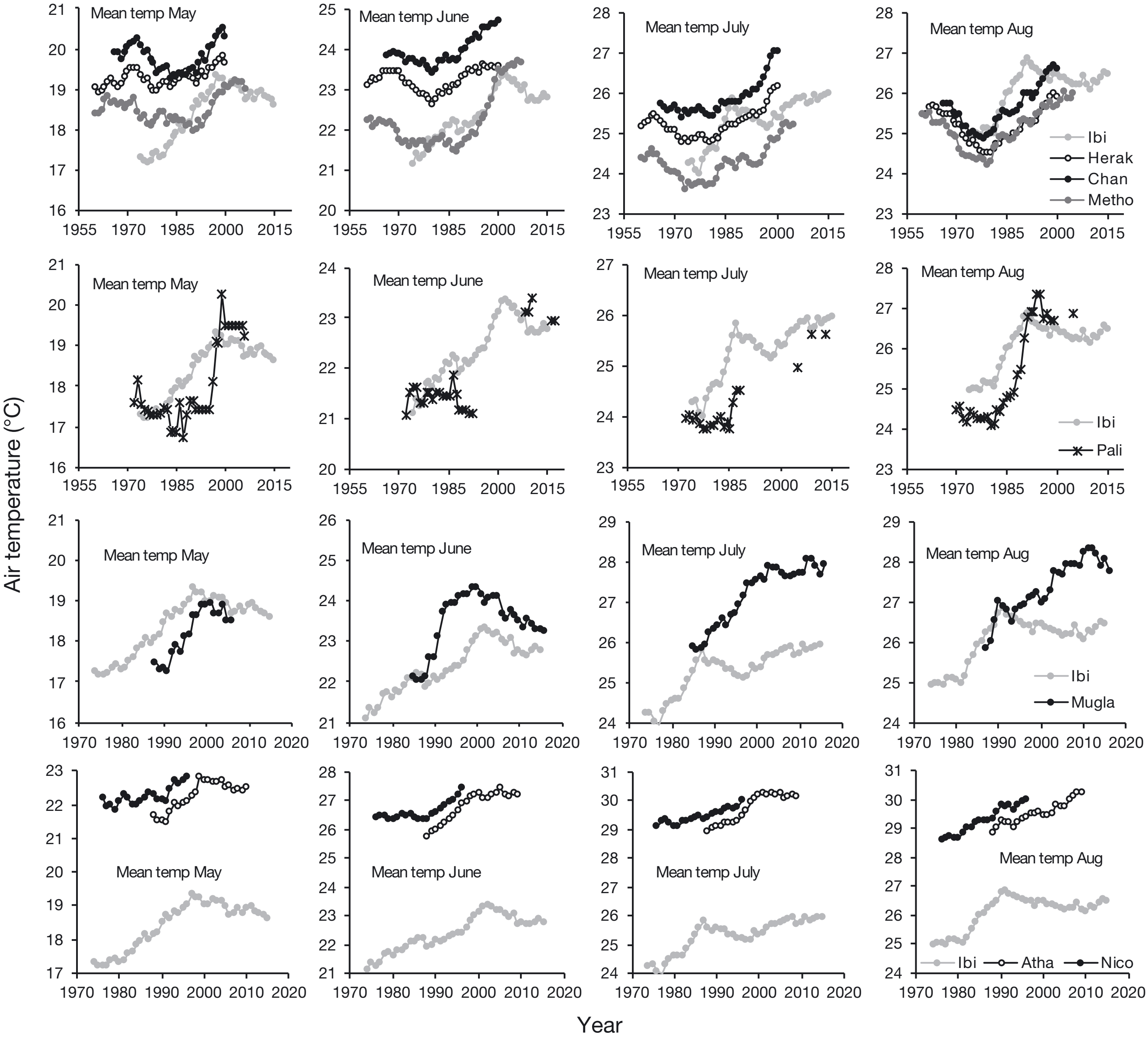

Fig. 5. Comparison between mean air temperatures (°C) recorded in the summer at the Balearic Islands (Ibiza), Italy (Palinuro) and several locations near loggerhead nesting beaches around the Mediterranean (Heraklion, Chania and Methoni, Greece; Mugla, Turkey; and Athalassa and Nicosia, Cyprus). Data are represented as 10 yr moving averages

($p < 0.05$) and August ($p < 0.01$), with more rain being recorded in Palinuro. In comparison to the easternmost sites, we found that the 2 western sites received significantly more rain than (1) Crete (Heraklion and Chania) (June–September for Ibiza and May–September for Palinuro) and (2) Nicosia (July–September for Ibiza and August–September for Palinuro) ($p < 0.05$ for all cases). There were no statistically significant differences in precipitation between Ibiza and Palinuro in any months ($p > 0.05$ for all cases).

No trends in precipitation were detected over time for Mallorca, Menorca, Palinuro, Heraklion and Nicosia for any months, and no trends were detected in May for any site ($p > 0.05$). In June, a Mann-Kendall test detected a change toward drier conditions in Ibiza ($p < 0.05$) and Chania ($p < 0.001$) and toward wetter conditions in Mugla ($p < 0.05$). A change was detected toward wetter conditions at Methoni in July ($p < 0.01$), Mugla in August ($p < 0.05$) and Ibiza in September ($p < 0.05$).

4. DISCUSSION

Comparing environmental conditions between areas where nesting sea turtle populations are well estab-

Table 4. Mean ± SD difference between the air temperature (°C) recorded at weather stations (Heraklion, Chania and Methoni in Greece; Mugla in Turkey; and Athalassa in Cyprus) located near important loggerhead turtle nesting beaches in the Mediterranean and air temperature on the island of Ibiza (Spain), where sporadic nesting has recently been recorded. Differences are in maximum, minimum and mean monthly air temperatures. Statistically significant differences are indicated (*$p < 0.05$, ***$p < 0.001$)

Month		Temperature difference (°C)				
		Methoni–Ibiza	Heraklion–Ibiza	Chania–Ibiza	Mugla–Ibiza	Athalassa–Ibiza
May	Max	−0.3 ± 1.2	1.1 ± 1.5***	1.9 ± 1.5***	2.2 ± 1.9***	6.8 ± 1.8***
	Min	0.5 ± 1.3	1.1 ± 1.2*	1.1 ± 1.2***	−3.1 ± 1.2***	0.3 ± 1.4
	Mean	0.1 ± 1.1	1.1 ± 1.3*	1.5 ± 1.3***	−0.5 ± 1.3	3.5 ± 1.5***
June	Max	−0.5 ± 1.1*	0.9 ± 1.5*	2.4 ± 1.4***	3.4 ± 1.6***	7.3 ± 1.2***
	Min	0.4 ± 0.9	1.2 ± 1.1***	1.4 ± 1.0***	−2.1 ± 1.3***	0.9 ± 1.3***
	Mean	0.0 ± 1.0	1.1 ± 1.2***	1.9 ± 1.2***	0.6 ± 1.3	4.1 ± 1.1***
July	Max	−1.4 ± 1.0***	−0.5 ± 1.6	1.2 ± 1.6*	4.4 ± 1.9***	7.4 ± 1.3***
	Min	−0.2 ± 1.0	1.1 ± 1.1	0.7 ± 1.2	−1.4 ± 1.3***	0.8 ± 1.2*
	Mean	−0.8 ± 0.9***	0.3 ± 1.2	1.0 ± 1.3*	1.4 ± 1.6***	4.1 ± 1.1***
Aug	Max	−1.1 ± 1.1***	−1.5 ± 1.3***	0.0 ± 1.2	4.0 ± 1.8***	6.6 ± 1.3***
	Min	−0.5 ± 1.1	0.2 ± 1.1	−0.4 ± 1.0	−2.3 ± 1.3***	−0.2 ± 1.3*
	Mean	−0.8 ± 1.0*	−0.7 ± 1.0*	−0.2 ± 1.0	0.8 ± 1.5*	3.2 ± 1.2***
Sept	Max	−0.6 ± 1.2*	−1.0 ± 1.7***	−0.1 ± 1.6	2.2 ± 1.7***	5.6 ± 1.6***
	Min	−0.7 ± 1.4*	0.1 ± 1.5	−0.3 ± 1.6	−4.3 ± 1.2***	−1.0 ± 1.4*
	Mean	−0.6 ± 1.2*	−0.5 ± 1.5*	−0.2 ± 1.5	−1.0 ± 1.3*	2.4 ± 1.2***

lished with others where nesting is sporadic can provide information about the suitability of new sites for successful nesting. Current climatic conditions in the western Mediterranean both on land and at sea appear to be suitable for loggerhead turtle nesting during the summer months. On the one hand, water temperature could allow development in the female oviduct for a long enough time to lay several clutches of eggs. On the other hand, air temperatures in the peak of summer are currently similar to those of some of the eastern sites, likely allowing egg incubation on suitable beaches. However, different climatic conditions in early and late summer could affect the duration of the nesting window in western areas.

Whereas hatchling production in tropical loggerhead turtle nesting populations could greatly be affected by climate change, temperate populations could be favored through an increase in hatching success (Pike 2014). Temperatures in sea turtle nests, and consequently hatching success and sex ratios, are affected by prevailing climatic conditions (Santidrián Tomillo et al. 2012). Nest temperature is generally highly correlated to air temperature (Laloë et al. 2021a), but large amounts of precipitation can also lower nest temperature due to the cooling effect of rain (Mrosovsky et al. 1984, Houghton et al. 2007, Esteban et al. 2016). Intense rain storms, such as those occurring in tropical areas, can lower nest temperatures by several degrees (Houghton et al. 2007, Esteban et al. 2016).

The time period for viable embryonic development is narrow in temperate areas because temperatures in spring and fall are too low for egg maturation and embryonic development. In the Mediterranean particularly, the time of nesting is highly constrained (Schofield et al. 2021), possibly due to thermal restrictions both on land and at sea. At Zakynthos, the time frame for optimal incubation is between 91 and 157 d, depending on the temperatures of the different nesting beaches (Katselidis et al. 2012). Air temperatures in early summer were cooler in the western Mediterranean, likely pushing nesting to later dates, in comparison to eastern sites. Although precipitation during the summer is very low in the Mediterranean (Philandras et al. 2011), we found that it was higher in September at western sites, as well as highly variable (0–245 mm in Ibiza and 0–191 mm in Palinuro). The highest values are still far from those of tropical beaches (Houghton et al. 2007, Santidrián Tomillo et al. 2012). However, considering that an effect of rain on nests has been observed in Greece (Rees & Margaritoulis 2004), where conditions are drier, we could expect a similar or stronger effect in the west. Therefore, cooler air temperatures at the beginning of summer, and precipitation at the end, could narrow the nesting window in western sites. We could expect a different effect of low temperatures at the beginning than at the end of the season. Because embryonic development in sea turtle eggs is arrested at low temperatures (Rafferty & Reina 2012), low temperatures in May–June could stop or delay development, but this could eventually resume as conditions warm up. However, rainfall at the end of

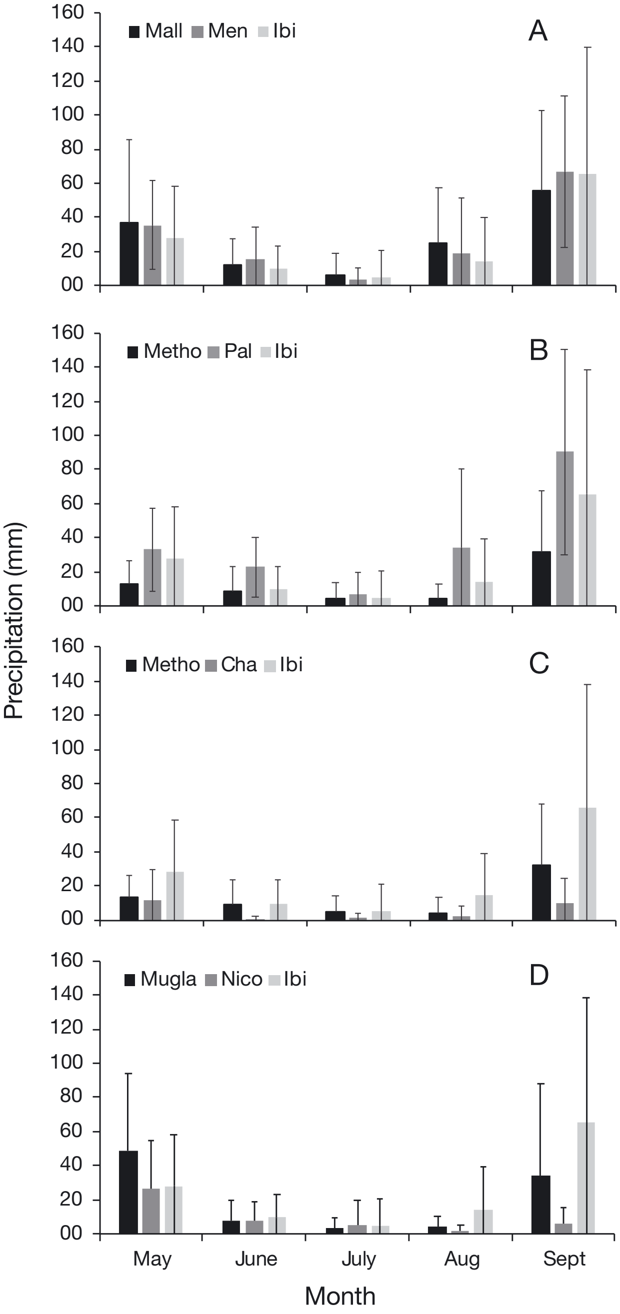

Fig. 6. Mean (±SD) precipitation (mm) accumulated per month between 1990 and 2010 recorded at (A) Mallorca, Menorca and Ibiza, Balearic Islands; (B) Methoni, Greece; Palinuro, Italy; and Ibiza; (C) Methoni, Chania, Greece; and Ibiza; and (D) Mugla, Turkey; Nicosia, Cyprus; and Ibiza

summer would add to the seasonal change toward cooler temperatures occurring in temperate areas during the summer–fall transition, likely resulting in egg mortality.

An important limitation of our study is the lack of nest/sand temperatures that would have allowed us to assess the influence of air temperatures obtained from weather stations on nests. Since some of the weather stations were located relatively far from the nesting beaches, local differences in climatic conditions could also have biased our results. Further research is needed on the specific thermal environment that western beaches can provide to properly assess suitability of these for egg development *in situ*. However, many of the clutches laid on western beaches have successfully hatched and produced viable hatchlings (Carreras et al. 2018), indicating that at least some beaches are suitable for sea turtle egg development. Suitable thermal ranges for egg development are ~25–35°C (Ackerman 1997), but ranges are likely to vary among populations (Howard et al. 2014). Specific thermal limits for egg incubation have not been defined for Mediterranean populations. However, air temperatures that allow incubation in the eastern basin could similarly do so on the western side. Since sea turtle nests from nearby nesting beaches can experience different thermal regimes (Zbinden et al. 2007, Weber et al. 2012), we could expect a similar variability in nest temperatures among western beaches depending on local beach characteristics.

Air temperatures at western sites fell within the cooler end of the thermal range in the Mediterranean, possibly influencing hatching success and sex ratios of natural clutches. Hatching success in sea turtle clutches is temperature-dependent, and low hatching success has been mainly related to high or extremely high incubation temperatures (Godley et al. 2001a, Valverde et al. 2010, Santidrián Tomillo et al. 2014, Martins et al. 2020), but low temperature could also be detrimental for egg incubation. Mean hatching success of loggerhead turtles in the eastern Mediterranean is relatively high (between 71.5 and 77%) at Zakynthos, Turkey and Cyprus (Kaska et al. 1998, Godley et al. 2001a, Margaritoulis 2005). In contrast, low hatching success resulting from low temperatures was reported at least for the first sporadic loggerhead nests recorded in Italy (Bentivegna et al. 2008, 2010) and Spain (Tomás et al. 2002), although factors other than temperature, e.g. tidal inundation, could have affected incubation (Tomás et al. 2002). Because thermal conditions vary across the nesting distribution, it is possible that low hatching success occurs at the warmest and coolest ends. Hatching success of green turtle *Chelonia mydas* clutches in Turkey has been projected to decline throughout the 21st century under climate change scenarios (Turkozan et al. 2021), and similar declines could possibly be expected in clutches of loggerhead turtles nesting in the same area. On the other hand, hatching success could gradually increase in cooler areas as climate moves toward more favorable thermal conditions for egg development, as has been suggested using climate change models (Pike 2014).

Due to lower temperatures, we can also expect that more male hatchlings will be proportionally produced in the western Mediterranean. Variability in sex ratios among established nesting populations occurs naturally, with primary sex ratios being female-biased at most nesting beaches but with a few beaches producing mainly male hatchlings (Baptistotte et al. 1999, Steckenreuter et al. 2010, Esteban et al. 2016). There is also seasonality in sex ratios, with males being typically produced at the beginning of the nesting season when temperatures are cooler (Mrosovsky 1984, Katselidis et al. 2012), as well as interannual variability with some male-biased years (Santidrián Tomillo et al. 2014).

Male-producing beaches are often located at the edge of the distribution range of a population (Baptistotte et al. 1999) and could serve as main providers of male turtles to a breeding population. For example, Marathonissi beach, within Zakynthos National Park, Greece, produces most of the male hatchlings in the population (Zbinden et al. 2007, Katselidis et al. 2012). Since nesting beaches in the eastern Mediterranean mostly produce female hatchlings (Hays et al. 2014), and considering that sex ratios could become extremely female-biased from climate warming, male-producing beaches could become critical for the viability of nesting populations (Hawkes et al. 2007b). This could be the case for some western Mediterranean beaches, especially considering that primary sex ratios are already highly female-biased in some of the easternmost beaches (e.g. Cyprus; Godley et al. 2001b). If turtles from the eastern and western basins mixed at foraging grounds and reproduced, the importance of western male-producing beaches would be beyond local, as they could act as a source of male turtles to other nesting areas in the Mediterranean. Satellite telemetry has revealed at least some level of exchange between eastern and western basins with some post-nesting females (ARCHELON unpubl. data) and a post-breeding male (Patel et al. 2012) from Greece traveling to foraging areas near Spain. A 1 yr old juvenile that was released along with 20 of its siblings in Spain also traveled to Greece in 2020 (García 2021).

Despite large differences in SST across the Mediterranean, SSTs in the small areas near the nesting beaches of Zakynthos, Ibiza and Palinuro were similar, at least over the last 40 yr. This time period coincides with the last warming period in SST in the Mediterranean. Because daily SST was only available since 1981, we do not know whether these similarities are recent. Mean SSTs at Ibiza were still lower in May (by 0.7–0.8°C) and June (by 0.8–1.1°C) than at the other sites. However, SST in Ibiza passed the 22°C threshold on average, only 8 d later than at Zakynthos (Table 3), further indicating that conditions are suitable for nesting at the 3 sites. Considering that SST was above the 22°C threshold for more than 60 d (and above the 26°C optimal threshold for part of that time), loggerhead turtles could potentially lay 3 or more clutches. This falls within the estimated number of clutches laid by loggerhead turtles in the Mediterranean (3.8 clutches at Kyparissia Bay, Greece, Rees et al. 2020; 3–5 clutches at Zakynthos, Schofield et al. 2021; and 2.2 clutches at Cyprus, Broderick et al. 2002). Other loggerhead populations, such as those nesting in Oman (Tucker et al. 2018) and Florida (Tucker 2010) lay more clutches (~5). Foraging conditions affect reproductive output in loggerhead turtles (Vander Zanden et al. 2014). Since sea turtles may not feed during the nesting season (Plot et al. 2013), even if climatic conditions allowed turtles to lay a higher number of clutches, they may not be able to do so if they did not have sufficient fat reserves. Intrinsic differences among populations and individuals may explain variability in clutch frequency.

Even if SST near the nesting beaches had been similar over a long time, large differences in SST between eastern and western basins could have still prevented nesting in the west. Nest-site fidelity cannot explain the occurrence of nesting at the western sites, because nests were seldom reported before the end of the 20th century (Maffucci et al. 2016, Carreras et al. 2018). Thus, nesting events must have been conditioned by the presence of adult turtles in the area, either at foraging grounds or as migrant travelers, which could also have been influenced by SST. Western areas are known to mainly provide foraging sites for juvenile loggerheads (Cardona et al. 2005). However, recent studies showed that they now also provide suitable foraging grounds for adult turtles (Almpanidou et al. 2022). In addition, foraging grounds of adult loggerheads in the Mediterranean are predicted to expand and shift toward the western basin due to climate warming (Chatzimentor et al. 2021). Using climate niche models, Chatzimentor et al. (2021) predicted that both juvenile and adult loggerheads are more likely to be present at foraging areas around the Balearic Islands and the Tyrrhenian Sea in the future, the 2 areas that we studied. It is possible that the occasional or increasing presence of adults in the area, together with suitable SST conditions during the summer, have allowed and triggered the occurrence of nesting events on western beaches. Sporadic nesting may also be occurring in southern Mediterranean countries that may go unnoticed. A loggerhead nest was recently recorded in Algeria for the first time (Benabdi & Belmahi 2020). Regional efforts to record region-wide scatter nesting would be very useful to quantify the extent of these nesting activities.

The only nesting event reported in Spain before the end of the 20th century was in 1870 (Carreras et al. 2018), coinciding with one of the warmest peaks in SST (Figs. 2 & 3). It is possible that more nests were laid during the first (around 1870) and second (mid-20th century) warming trends in the Mediterranean that went undetected, because human presence on most beaches was sporadic and nests were unlikely to be reported before the boom in tourism. There are now more people than ever on beaches with rapid access to technology and social media, increasing the probability of nest detection. Moreover, there is a growing number of research groups and environmental offices, both regional and national, increasing monitoring effort and creating campaigns to detect nesting events, particularly since 2014.

On the other hand, the number of nests in the western Mediterranean could have also increased due to a recovery of the Mediterranean and Atlantic populations since both Mediterranean and Atlantic turtles use the western Mediterranean as feeding grounds (Clusa et al. 2014 and references therein). Mediterranean loggerhead turtles are now regionally classified as Least Concern by the International Union for Conservation of Nature and Natural Resources, and the number of nests shows a slightly positive trend (Casale 2015, Casale et al. 2018). These 2 hypotheses may not be mutually exclusive. However, because the loggerhead turtles that nest in the western Mediterranean are of mixed origin, with some individuals belonging to Atlantic populations and others to the Mediterranean one (Clusa et al. 2014, Carreras et al. 2018), it seems more plausible that nesting in the western Mediterranean is linked to a shift to optimal thermal conditions.

As sea turtles are long-lived and late maturing (Casale et al. 2011, Scott et al. 2012), it may take 20–30 yr for hatchlings emerged from western beaches to come back to nest as mature females, assuming these turtles will be more philopatric than their mothers and will come back to the same area. First-time nesters may disperse more than older turtles (Tucker 2010), and it is possible that once new nesters select a suitable beach, they come back to the same place in subsequent seasons, completing the colonization process. Through comparison of air and oceanic temperatures in different areas and historical times, we have made a first attempt to describe the potential influence of air and sea warming trends in the recent distribution of nests of loggerhead turtles in the Mediterranean. Considering the long generation time in sea turtles, research in the western Mediterranean over the next couple of decades will likely shed light into how colonization of new nesting habitats occurs in sea turtles for the successful establishment of nesting populations.

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LITERATURE CITED

Ackerman RA (1997) The nest environment and the embryonic development of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 83–106

Almpanidou V, Tsapalou V, Chatzimentor A, Cardona L and others (2022) Foraging grounds of adult loggerhead sea turtles across the Mediterranean Sea: key sites and hotspots of risks. Biodivers Conserv 31:143–160

Anderson RP (2013) A framework for using niche models to estimate impacts of climate change on species distributions. Ann NY Acad Sci 1297:8–28

Baltazar-Soares M, Klein JD, Correia SM, Reischig T and others (2020) Distribution of genetic diversity reveals colonization patterns and philopatry of the loggerhead sea turtles across geographic scales. Sci Rep 10:18001

Baptistotte C, Scalfoni JT, Mrosovsky N (1999) Male-producing thermal ecology of a southern loggerhead turtle nesting beach in Brazil: implications for conservation. Anim Conserv 2:9–13

Benabdi M, Belmahi AE (2020) First record of loggerhead turtle (*Caretta caretta*) nesting in the Algerian coast (southwestern Mediterranean). J Black Sea Mediterr Environ 26:100–105

Bentivegna F, Treglia G, Hochscheid S (2008) The first report of a loggerhead turtle *Caretta caretta* nest on the central Tyrrhenian coast (western Mediterranean). Mar Biodivers Rec 1:e14

Bentivegna F, Rasotto MB, De Lucia GA, Secci E and others (2010) Loggerhead turtle (*Caretta caretta*) nests at high latitudes in Italy: a call for vigilance in the western Mediterranean. Chelonian Conserv Biol 9:283–289

Blanco GS, Morreale SJ, Seminoff JA, Paladino FV, Piedra R, Spotila JR (2013) Movements and diving behavior of internesting green turtles along Pacific Costa Rica. Integr Zool 8:293–306

Bowen BW, Karl SA (2007) Population genetics and phylogeography of sea turtles. Mol Ecol 16:4886–4907

Broderick AC, Glen F, Godley BJ, Hays GC (2002) Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. Oryx 36:227–235

Cardona L, Revelles M, Carreras C, San Félix M, Gazo M, Aguilar A (2005) Western Mediterranean immature loggerhead turtles: habitat use in spring and summer assessed through satellite tracking and aerial surveys. Mar Biol 147:583–591

Carreras C, Pascual M, Tomás J, Marco A and others (2018) Sporadic nesting reveals long distance colonisation in the philopatric loggerhead sea turtle (*Caretta caretta*). Sci Rep 8:1435

Casale P (2015) Loggerhead turtle *Caretta caretta* (Mediterranean subpopulation). The IUCN Red List of Threatened Species 2015: e.T83644804A83646294. https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T83644804A83646294.en.

Casale P, Mazaris AD, Freggi D (2011) Estimation of age at maturity of loggerhead sea turtles *Caretta caretta* in the Mediterranean using length-frequency data. Endang Species Res 13:123–129

Casale P, Broderick AC, Camiñas JA, Cardona L and others (2018) Mediterranean sea turtles: current knowledge and priorities for conservation and research. Endang Species Res 36:229–267

Chatzimentor A, Almpanidou V, Doxa A, Dimitriadis C, Mazaris AD (2021) Projected redistribution of sea turtle foraging areas reveals important sites for conservation. Clim Change Ecol 2:100038

Clusa M, Carreras C, Pascual M, Demetropoulos A and others (2013) Mitochondrial DNA reveals Pleistocenic colonisation of the Mediterranean by loggerhead turtles (*Caretta caretta*). J Exp Mar Biol Ecol 439:15–24

Clusa M, Carreras C, Pascual M, Gaughran SJ and others (2014) Fine-scale distribution of juvenile Atlantic and Mediterranean loggerhead turtles (*Caretta caretta*) in the Mediterranean Sea. Mar Biol 161:509–519

Dodd CK Jr (1988) Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). Biol Rep 88(14). FA0 Synopsis NMFS-149. US Fish and Wildlife Service, US Department of the Interior, Washington, DC

Esteban N, Laloë JO, Mortimer JA, Guzman A, Hays GC (2016) Male hatchling production in sea turtles from one of the world's largest marine protected areas, the Chagos Archipelago. Sci Rep 6:20339

García P (2021) El largo viaje de una tortuga marina marcada en Murcia. Quercus 428:51–52

Godley BJ, Broderick AC, Downie JR, Glen F and others (2001a) Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatchling production in the Mediterranean. J Exp Mar Biol Ecol 263:45–63

Godley BJ, Broderick AC, Mrosovsky N (2001b) Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations. Mar Ecol Prog Ser 210:195–201

González-Paredes D, Fernández-Maldonado C, Grondona M, Martínez-Valverde R, Marco A (2021) The western most nest of a loggerhead sea turtle, *Caretta caretta* (Linnaeus 1758), registered in the Mediterranean Basin (Testudines, Cheloniidae). Herpetol Notes 14:907–912

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007a) Only some like it hot – quantifying the environmental niche of the loggerhead sea turtle. Divers Distrib 13:447–457

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007b) Investigating the potential impacts of climate change on a marine turtle population. Glob Change Biol 13:923–932

Hays GC, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD (2002) Water temperature and internesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. J Therm Biol 27:429–432

Hays GC, Mazaris AD, Schofield G (2014) Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. Front Mar Sci 1:43

Heppell SS (1998) Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367–375

Hill JE, Robinson NJ, King CM, Paladino FV (2017) Diving behavior and thermal habitats of gravid hawksbill turtles at St Croix, USA. Mar Biol 164:17

Hochscheid S, Bentivegna F, Hays GC (2005) First records of dive durations for a hibernating sea turtle. Biol Lett 1:82–86

Houghton JDR, Myers AE, Lloyd C, King RS, Isaacs C, Hays GC (2007) Protracted rainfall decreases temperature within leatherback turtle (*Dermochelys coriacea*) clutches in Grenada, West Indies: ecological implications for a species displaying temperature dependent sex determination. J Exp Mar Biol Ecol 345:71–77

Howard R, Bell I, Pike DA (2014) Thermal tolerances of sea turtle embryos: current understanding and future directions. Endang Species Res 26:75–86

Kaska Y, Downie R, Tippett R, Furness RW (1998) Natural temperature regimes for loggerhead and green turtle nests in the eastern Mediterranean. Can J Zool 76: 723–729

Katselidis KA, Schofield G, Stamou G, Dimopoulos P, Pantis JD (2012) Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. Anim Conserv 15:508–518

Laloë JO, Chivers WJ, Esteban N, Hays GC (2021a) Reconstructing past thermal conditions in beach microclimates. Glob Change Biol 27:6592–6601

Laloë JO, Tedeschi JN, Booth DT, Bell I, Dunstan A, Reina RD, Hays GC (2021b) Extreme rainfall events and cooling of sea turtle clutches: implications in the face of climate warming. Ecol Evol 11:560–565

Leighton PA, Horrocks JA, Kramer DL (2011) Predicting nest survival in sea turtles: When and where are eggs most vulnerable to predation? Anim Conserv 14:186–195

Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, Grenouillet G (2020) Species better track climate warming in the oceans than on land. Nat Ecol Evol 4: 1044–1059

Levinsky I, Skov F, Svenning JC, Rahbek C (2007) Potential impacts of climate change on the distributions and diversity patterns of European mammals. Biodivers Conserv 16:3803–3816

Maffucci F, Corrado R, Palatella L, Borra M and others (2016) Seasonal heterogeneity of ocean warming: a mortality sink for ectotherm colonizers. Sci Rep 6:23983

Margaritoulis D (2005) Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. Chelonian Conserv Biol 4:916–929

Martins S, Silva E, Abella E, de Santos Loureiro N, Marco A (2020) Warmer incubation temperature influences sea turtle survival and nullifies the benefit of a female-biased sex ratio. Clim Change 163:689–704

Mayne B, Tucker AD, Berry O, Jarman S (2020) Lifespan estimation in marine turtles using genomic promoter CpG density. PLOS ONE 15:e0236888

Miller JD, Limpus CJ, Godfrey MH (2003) Nest site selection, oviposition, eggs, development, hatching and emergence of loggerhead turtles. In: Bolten A, Witherington B (eds) Loggerhead sea turtles. Smithsonian Institution Press, Washington, DC, p 125–143

Montero N, Santidrián Tomillo P, Saba V, Marcovaldi MAG, López-Mendilaharsu M, Santos AS, Fuentes MMPB (2019) Effects of local climate on loggerhead hatchling production in Brazil: implications from climate change. Sci Rep 9:8861

Mrosovsky N (1984) Sex ratio of sea turtles: seasonal trends. Science 225:739–741

Mrosovsky N, Hopkins-Murphy SR, Richardson JI (1984) Sex ratio of sea turtles: seasonal changes. Science 225: 739–741

Mrosovsky N, Kamel S, Rees AF, Margaritoulis D (2002) Pivotal temperature for loggerhead turtles (*Caretta caretta*) from Kyparissia Bay, Greece. Can J Zool 80:2118–2124

Patel SH, Panagopoulou A, Morreale SJ, Paladino FV, Margaritoulis D, Spotila JR (2012) Post-reproductive migration of an adult male loggerhead from Crete revealed by satellite telemetry. In: Proc 32nd Annu Symp Sea Turtle Biology and Conservation, 11–16 March 2012, Huatulco, Mexico

Pecl GT, Araújo MB, Bell JD, Blanchard J and others (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355: eaai9214

Philandras CM, Nastos PT, Kapsomenakis J, Douvis KC, Tselioudis G, Zerefos CS (2011) Long term precipitation trends and variability within the Mediterranean region. Nat Hazards Earth Syst Sci 11:3235–3250

Pike DA (2014) Forecasting the viability of sea turtle eggs in a warming world. Glob Change Biol 20:7–15

Plot V, Jenkins T, Robin JP, Fossette S, Georges JY (2013) Leatherback turtles are capital breeders: morphometric and physiological evidence from longitudinal monitoring. Physiol Biochem Zool 86:385–397

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W and others (2013) Global imprint of climate change on marine life. Nat Clim Change 3:919–925

Rafferty AR, Reina RD (2012) Arrested embryonic development: a review of strategies to delay hatching in egg-laying reptiles. Proc R Soc B 279:2299–2308

Rees AF, Margaritoulis D (2004) Beach temperatures, incubation durations and estimated hatchling sex ratio for loggerhead sea turtle nests in southern Kyparissia Bay, Greece. Testudo 6:23–36

Rees AF, Theodorou P, Margaritoulis D (2020) Clutch frequency for loggerhead turtles (*Caretta caretta*) nesting in Kyparissia. Herpetol Conserv Biol 15:131–138

Salmon M (2006) Protection of sea turtles from artificial night lighting at Florida's oceanic beaches. In: Rich C, Longcore T (eds) Ecological consequences of artificial night lighting. Island Press, Washington, DC, p 141–168

Santidrián Tomillo P, Saba VS, Blanco GS, Stock CA, Paladino FV, Spotila JR (2012) Climate driven egg and hatchling mortality threaten survival of Eastern Pacific leatherback turtles. PLOS ONE 7:e37602

Santidrián Tomillo P, Oro D, Paladino FV, Piedra R, Sieg AE, Spotila JR (2014) High beach temperatures increased female-biased primary sex ratios but reduced output of female hatchlings in the leatherback turtle. Biol Conserv 176:71–79

Sato K, Matsuzawa Y, Tanaka H, Bando T, Minamikawa S, Sakamoto W, Naito Y (1998) Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas,* are affected by temperature. Can J Zool 76:1651–1662

Schofield G, Bishop CM, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2009) Microhabitat selection by sea turtles in a dynamic thermal environment. J Anim Ecol 78: 14–21

Schofield G, Katselidis KA, Lilley KS, Reina RD, Hays GD (2017) Detecting elusive aspects of wildlife ecology using drones: new insights on the mating dynamics and operational sex ratios of sea turtles. Funct Ecol 31:2310–2319

Schofield G, Dickson LCD, Westover L, Dujon AM, Katselidis KA (2021) COVID-19 disruption reveals mass-tourism pressure on nearshore sea turtle distributions and access to optimal breeding habitat. Evol Appl 14: 2516–2526

Scott R, Marsh R, Hays GC (2012) Life in the really slow lane: loggerhead sea turtles mature late relative to other reptiles. Funct Ecol 26:227–235

Standora EA, Spotila JR (1985) Temperature dependent sex determination in sea turtles. Copeia 1985:711–722

Steckenreuter A, Pilcher N, Krüger B, Ben J (2010) Male-biased primary sex ratio of leatherback turtles (*Dermochelys coriacea*) at the Huon Coast, Papua New Guinea. Chelonian Conserv Biol 9:123–128

Stiebens VA, Merino SE, Roder C, Chain FJJ, Lee PLM, Eizaguirre C (2013) Living on the edge: how philopatry maintains adaptive potential. Proc R Soc B 280:20130305

Storch S, Wilson RP, Hillis-Starr ZM, Adelung D (2005) Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle *Eretmochelys imbricata.* Mar Ecol Prog Ser 293:263–271

Tomás J, Mons JL, Martin JJ, Bellido JJ, Castillo JJ (2002) Study of the first reported nest of loggerhead sea turtle, *Caretta caretta*, in the Spanish Mediterranean coast. J Mar Biol Assoc UK 82:1005–1007

Tomás J, Gazo M, Álvarez C, Gozalbes P, Perdiguero D, Raga JA, Alegre F (2008) Is the Spanish coast within the regular nesting range of the Mediterranean loggerhead sea turtle (*Caretta caretta*)? J Mar Biol Assoc UK 88: 1509–1512

Tucker AD (2010) Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock estimation. J Exp Mar Biol Ecol 383:48–55

Tucker AD, Baldwin R, Willson A, Kiyumi AA and others (2018) Revised clutch frequency estimates for Masirah Island loggerhead turtle (*Caretta caretta*). Herpetol Conserv Biol 13:158–166

Turkozan O, Almpanidou V, Yilmaz C, Mazaris AD (2021) Extreme thermal conditions in sea turtle nests jeopardize reproductive output. Clim Change 167:30

Valverde RA, Wingard S, Gómez F, Tordoir MT, Orrego CM (2010) Field lethal incubation temperature of olive ridley sea turtle *Lepidochelys olivacea* embryos at a mass nesting rookery. Endang Species Res 12:77–86

Valverde-Cantillo V, Robinson NJ, Santidrián Tomillo P (2019) Influence of oceanographic conditions on nesting abundance, phenology and internesting periods of east Pacific green turtles. Mar Biol 166:93

Vander Zanden HB, Pfaller JB, Reich KJ, Pajuelo M and others (2014) Foraging areas differentially affect reproductive output and interpretation of trends in abundance of loggerhead turtles. Mar Biol 161:585–598

Weber SB, Blount JD, Godley BJ, Witt MJ, Broderick AC (2011) Rate of egg maturation in marine turtles exhibits 'universal temperature dependence'. J Anim Ecol 80: 1034−1041

Weber SB, Broderick AC, Groothuis TGG, Ellick J, Godley BJ, Blount JD (2012) Fine-scale thermal adaptation in a green turtle nesting population. Proc R Soc B 279:1077−1084

Weishampel JF, Bagley DA, Ehrhart LM (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. Glob Change Biol 10:1424−1427

Zbinden JA, Davy C, Margaritoulis D, Arlettaz R (2007) Large spatial variation and female bias in the estimated sex ratio of loggerhead sea turtle hatchlings of a Mediterranean rookery. Endang Species Res 3:305−312

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