



## Original research article

# Going west: Range expansion for loggerhead sea turtles in the Mediterranean Sea under climate change

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## ABSTRACT

Global changes represent possibly the greatest threat to the future of biodiversity, and this is especially true for species using very different habitats during their life cycle. The problem is even greater when dealing with human dominated landscapes (e.g., the Mediterranean basin) where climate change and habitat destruction and degradation often interact synergistically. We explored this synergy focusing on loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea. Sea turtles depend on both marine and terrestrial environments and are influenced at the same time by changes occurring in both realms. To explore the changes of nesting grounds in the last decades, we first analysed the changes in the 10-year geographical centers of gravity for all nests from 1960 to 2020. By focusing only of the last 20 years, we incorporated both terrestrial and marine variables into a species distribution model (SDM), while accounting for temporal variability by using a multi-temporal calibration approach. The center of gravity for all nesting grounds shifted roughly of 1300 km to the northwest, and the climate suitability model (with the lowest AICc value and a mean AUC =  $0.919 \pm 0.047$ ; p-value  $\leq 0.001$ ) highlighted a sharp increase over time in the northwest Mediterranean Sea. In the same time frame, the southeast Mediterranean showed a very limited increase in climate suitability for nesting. The most important variables were anthropogenic variables, which negatively influence nesting probability, and sea surface temperature, with an increase up to a maximum probability of nesting around 24–25 °C, but a rapid decrease at higher temperatures. The potential importance of the North-western Mediterranean beaches as possible nesting range for sea turtles highlights the relevance of proactive efforts to assist sea turtles' conservation during their range expansion. More in general, our analyses demonstrate the importance of considering variables from multiple realms when modeling the distribution of species with complex life cycles.

## 1. Introduction

The Mediterranean basin, including both the sea and the land, is certainly one of the most vulnerable regions in the world, being heavily impacted by historical and recent anthropogenic changes and representing a hotspot of both biodiversity and future global changes (Underwood et al., 2009). Human activities, climate change and the invasion of alien species, often in synergy with overfishing, pollution, and eutrophication, are threatening the rich marine life of the Mediterranean Sea more than any other sea or ocean

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(Coll et al., 2010). Also, coastal systems are particularly threatened because of urbanization and tourism development (Grenon and Batisse, 1989; Vogiatzakis et al., 2005), with coasts being almost completely encroached with buildings and infrastructures, and with roughly 450 million of residents and a constantly growing presence of tourists in summer months (UNEP-RAC, 1995).

Future climate warming is projected to be strong, particularly during summer times (Pastor et al., 2020), but climate change is already hitting the area extensively. Annual mean temperatures on Mediterranean lands are already overshooting the target of the Paris Agreement, being 1.5 °C higher than in pre-industrial times (Cramer et al., 2018; MedECC, 2020). The average sea surface temperature (SST) is following a similar path, with a constant increase from 1978 to 2003 (overall average increase = 1.4 °C; Belkin, 2009), particularly in the eastern part of the basin (Skliris et al., 2012).

Several studies have explored the effects of global changes on Mediterranean biodiversity, but all focused on terrestrial (e.g., Maiorano et al., 2011), marine (e.g., Field et al., 2010) or freshwater systems (e.g., He et al., 2019) as isolated one from the other. The three systems are, however, strictly interconnected, with threats acting on marine ecosystems that are going to have an impact on terrestrial coastal areas (Häkkinen et al., 2021), and the same for freshwater systems (Cianfrani et al., 2011). A few species are paradigmatic examples of this complexity, spanning in their ecology different systems (e.g., marine and terrestrial habitats) and potentially being exposed to multiple threats in different phases of their life cycle (Häkkinen et al., 2021). A clear example is provided by sea turtles, which spend their entire life in marine environments but nest on land along the coasts, have a migratory life stage, and a sex determination that is based on incubation temperature, therefore depending directly on ambient temperature on land (Pritchard et al., 1997). Three species of sea turtles are present in the Mediterranean basin (Casale, 2010): the leatherback turtle (*Dermochelys coriacea*), the green turtle (*Chelonia mydas*), and the loggerhead turtle (*Caretta caretta*). While the leatherback turtle is only present with vagrant individuals, probably of Atlantic origin (Lescure et al., 1989; Laurent, 1998), the other two species regularly breed along the Mediterranean shores with limited gene flow towards the Atlantic populations (Encalada et al., 1996; Laurent et al., 1998).

The effects of global changes are going to hit sea turtles in multiple ways. Sea level rise is already contributing to the loss of beach and sea turtle nesting habitat (Fuentes et al., 2011; Dimitriadis et al., 2022), and extreme weather events contribute even further to beach erosion (Vousdoukas et al., 2020; Turkozan et al., 2021). The increasing temperatures directly translates into hotter sand, and this has the potential to alter sex ratio (and therefore population biology patterns) for species with a temperature-based sex determination. Theoretically hotter temperatures will translate into higher proportion of female hatchlings (Lalœ et al., 2016), but extreme hot summers can lead to decreased hatchling rates or even to complete nest failures (Pike, 2014). Global changes are also altering ocean currents (Rahmstorf, 1997), which play an important role in animal dispersal (Lohmann et al., 2008; Witt et al., 2010), can influence juveniles during the so called "lost years" (i.e., the early life stage in which the knowledge on ecology and distribution of sea turtles is almost null; Hamann et al., 2013), and can alter foraging areas (Bjorndal, 1985; Davenport, 1998; Polovina et al., 2004).

The knowledge we have on the impact of climate changes on sea turtles has increased in the last decades, but often remains limited to local or regional settings (e.g., Patel et al., 2016; Varela et al., 2019). However, the Mediterranean basin is characterized by a high level of social and political fragmentation, both on land and in the sea (Micheli et al., 2013; Liu et al., 2020), and a basin wide focus on the effects of global changes on sea turtles would be of the outmost importance for any current and/or future conservation and management plan.

To better understand the effects of global changes on coastal systems in the Mediterranean basin we focused our analyses on the Loggerhead turtle which is widely distributed throughout the entire Mediterranean basin. Adults and juveniles are present in the entire basin, concentrating in foraging areas along the North Adriatic and Central Mediterranean continental shelves, with lower frequencies in the southern Ionian and in the area between Sicily and Tunisia (Bolten and Witherington, 2004; Casale et al., 2007, 2020; Cambie et al., 2013). Nesting areas, on the contrary, are mainly concentrated in the eastern Mediterranean, although a few authors (using genetic analyses on the sporadic nesting events in the western Mediterranean) have suggested a trend in recent years towards an increased number of nests also in the western basin (Carreras et al., 2018) hypothesizing a response of the species to the ongoing climate change.

We tested the robustness of this trend building an extensive database on nest locations going back in time to the 1960s. Then we explored the factors (climatic and environmental) related to the changes in distribution that we measured. Therefore, we first analyzed the changes in the distribution of known nests from 1960 to 2020 and then, focusing only of the last 20 years and using a multi-temporal species distribution model (*sensu* Maiorano et al., 2013), we built yearly maps of potential species presence in nesting grounds. We included in model calibration all factors which can influence turtle nesting behaviors, considering both marine and terrestrial covariates, and including human driven (e.g., nighttime light) as well as physical factors (e.g., sea surface temperature).

## 2. Methods

### 2.1. Nesting locations and environmental data

We searched Web of Science, Scopus, and Google Scholar for peer review papers, technical reports, and grey literature (hereafter "papers") using the following search clauses: "*Caretta caretta* nesting habitat", "*Caretta caretta* range shift", "*Caretta caretta* Mediterranean Sea", "*Caretta caretta* climate change", "*Caretta caretta* species distributions", "Loggerhead sea turtle nesting habitat", "Loggerhead sea turtle range shift", "Loggerhead sea turtle Mediterranean Sea", "Loggerhead sea turtle climate change", "Loggerhead sea turtle species distributions". We scanned all documents searching for any available indication on nest locations, and we considered also all literature cited in these articles (see complete list in Appendix A in Supplementary Material, Tab. A.1). We excluded all dubious observations (nest attempted, nest possible but not proved, false crawls) and duplicate records (same date and same beach reported in different documents).

To model the potential distribution for nesting sites we considered both environmental and climatic variables spanning the marine

and the terrestrial realm (Häkkinen et al., 2021) for a total of 14 variables (Table 1; Sbrocco and Barber, 2013; Fratianni et al., 2014; Falchi et al., 2016; CIESIN, 2018; European Commission JRC, 2019; Teruzzi et al., 2019). All variables were selected considering the species' nesting ecology and data availability (Lutz et al., 2002; Bolten and Witherington, 2004) and were summarized over May–September to cover specifically the nesting season (Pastor et al., 2019).

Temperature is probably the most important climatic factor in turtle population biology. On land temperature influences sex determination, incubation duration, and hatching success (Yntema and Mrosovsky, 1980; Mrosovsky et al., 1995; Broderick et al., 2000; Hays et al., 2003; Godley et al., 2003). In the sea, the spatial distribution of adults is strictly correlated to sea surface temperature (SST; Spotila and Standora, 1985; Seebacher and Franklin, 2005) which can influence the choice of nesting grounds (Mazaris et al., 2004; Hawkes et al., 2007) and is related to both inter-nesting intervals and to the number of nests per year (Sato et al., 1998; Solow et al., 2002; Hays et al., 2003; Mazaris et al., 2008). Besides SST, we also considered several variables related to water chemistry that can influence positively and/or negatively the choice of nesting grounds for sea turtles in the Mediterranean (Table 1; Lutz et al., 2002; Bolten and Witherington, 2004). The excessive concentration of nitrogen and phosphorus used in agriculture causes water pollution, eutrophication, and acidification (Ngatia et al., 2019), which thus negatively affect the life of sea turtles, destroying feeding habitats, and consequently nesting habitats (Lutcavage, 2017). On the contrary, the concentration of dissolved oxygen in sea water was selected as a fundamental parameter to establish the degree of health of a water body (Bozorg-Haddad, 2021). Poor water quality may lead to the declined health of sea turtles, changing their distribution (Brodie et al., 2014). Finally, the concentration of chlorophyll, phytoplankton and net primary production can be used to estimate the abundance of nutrition available for the species (Felip and Catalan, 2000).

The choice of a particular beach as nesting ground is not linked to the presence of a particular type of sand (Patino-Martinez et al., 2022) but it is negatively influenced by urbanization and other types of development (Casale, 2010). In fact, turtles must compete for their nests with tourists and coastal residents, being often forced to use suboptimal nesting habitats or even to waist their eggs in the sea (Witherington and Martin, 2000; Vandersteen et al., 2020). Furthermore, human encroachments completely alter the natural patterns of night-time lights. Lightings near the shore can disorient hatchlings and cause inland wandering, often resulting in death (Price et al., 2018; Hu et al., 2018). Therefore, on land, we considered variables such as presence of sandy coasts, human population density, and artificial lights (Table 1).

To provide a better approximation of the animals' perception of their environment (*sensu* Falcucci et al., 2009), we used a circular moving window to run a map algebra focal function for each pixel of the study area and for each layer. For marine variables we considered a 20 km radius window, while for terrestrial variables we chose a 2 km radius. The two different radii were chosen to account for the mobility of the animals that swim within a mean distance of 20 Km from beaches during nesting season (Chambault et al., 2016; Sloan et al., 2022), and for the limited movements close to the shore ( $\pm 2$  km) (Hart et al., 2010). For all variables, the focal function assigned to the central pixel of the window (always a coastal pixel) the mean value calculated over all pixels inside the window. To limit negative effects of multicollinearity on the final model (Araújo et al., 2019), we performed a Variance Inflation Factor analysis (VIF) on the initial set of 14 variables and we excluded all variables with a  $VIF \geq 3$  obtaining a final database with 10 variables.

**Table 1**

Complete set of environmental and climatic variables, with their spatial and temporal resolution, and source.

Environmental and climatic variables	Spatial resolution	Time series	References and Source
sea surface temperature (sst) [°C]	7 × 7 km	1955–2015	<a href="https://doi.org/10.25423/medsea_reanalysis_phy_006_009">https://doi.org/10.25423/medsea_reanalysis_phy_006_009</a>
salinity (psu) [psu]	7 × 7 km	1955–2015	<a href="https://doi.org/10.25423/medsea_reanalysis_phy_006_009">https://doi.org/10.25423/medsea_reanalysis_phy_006_009</a>
concentration of chlorophyll in sea water (chl) [mg/m <sup>3</sup> ]	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
concentration of phytoplankton in seawater (phyc) [mmol/m <sup>3</sup> ]	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
concentration of dissolved oxygen in seawater (O <sub>2</sub> ) [mmol/m <sup>3</sup> ]	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
concentration of nitrate (NO <sub>3</sub> ) [mmol/m <sup>3</sup> ] and phosphate (PO <sub>4</sub> ) [mmol/m <sup>3</sup> ] in seawater	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
net primary production in sea (pp) [mol/m <sup>3</sup> /s]	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
oceanic pH (pH) [pH]	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
partial pressure of carbon dioxide (pCO <sub>2</sub> ) [Pa]	10 × 10 km	1999–2017	<a href="https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008">https://doi.org/10.25423/MEDSEA_REANALYSIS_BIO_006_008</a>
bathymetry (bathy) [m]	1 × 1 km	2000, 2005, 2010, 2015	<a href="https://doi.org/10.1890/12-1358.1">https://doi.org/10.1890/12-1358.1</a>
sandy coastlines (beach) [m]	250 m	/	<a href="http://data.europa.eu/89h/18eb5f19-b916-454f-b2f5-88881931587e">http://data.europa.eu/89h/18eb5f19-b916-454f-b2f5-88881931587e</a>
human population (pop) [number of persons per pixel]	1 × 1 km	2000, 2005, 2010, 2015	<a href="https://doi.org/10.7927/H4JW8BX5">https://doi.org/10.7927/H4JW8BX5</a>
artificial night sky brightness (light) [mcd/m <sup>2</sup> ]	1 × 1 km	/	<a href="http://doi.org/10.5880/GFZ.1.4.2016.001">http://doi.org/10.5880/GFZ.1.4.2016.001</a>

## 2.2. Changes in nest distribution

To estimate the changes in the spatial distribution of nests we divided the Mediterranean basin into 7 ecoregions (Spalding et al., 2007): Adriatic Sea, Aegean Sea, Levantine Sea, Tunisian Plateau/Gulf of Sidra, Ionian Sea, Western Mediterranean, and Alboran Sea. We analysed changes in the distribution of the nests considering 10 years intervals. In this way we tried to avoid any emphasis in our results on year-to-year variations which can be linked to particular events or to sampling artefacts. Starting from the first decade of available data (1960–1969), we measured for each decade the presence of nesting loggerhead turtles in each ecoregion.

Furthermore, considering all beaches with nesting turtles, we calculated the center of gravity of the distribution for each decade and we measured the change (Euclidean distance) and direction (degrees relative to north) in consecutive centers of gravity.

We acknowledge that sampling bias can potentially be a problem for our database and analyses, especially considering a time frame spanning more than 50 years. In fact, we cannot exclude that any eventual change in distribution is linked to a change in sampling effort. To exclude this possibility, we considered the amount of effort in the scientific research and citizen science devoted to Mediterranean Sea and species distributions over the years. We searched Web of Science, Scopus, and Google Scholar for documents corresponding to the following research terms: “Mediterranean Sea” and “species distribution”. Then, for each decade considered, we calculated the share of papers dealing with loggerhead distribution (corresponding to the total number of papers available in our database) over the total number of papers retrieved. We tested for the presence of a temporal trend in the share calculating the Pearson correlation between shares and decades. The absence of a temporal trend in the share would clearly indicate that the focus on sea turtle distribution did not change over time.

## 2.3. Nesting model

We modeled potential nesting probability for the loggerhead turtle in the Mediterranean using a maximum entropy algorithm (Maxent v. 3.4.1; Phillips et al., 2017). We used a multi-temporal calibration approach (*sensu* Maiorano et al., 2013) coupling each nesting location with climate/environmental data corresponding to the same nesting period from 2000 to 2015. For each time step, we added random background points following a 10:1 ratio over available occurrences. The total number of background points summed up to 10,000 locations and covered the entire Mediterranean coast. We tuned model parameters following Muscarella et al. (2014), with regularization multiplier ranging from 0.5 to 5.0 (0.5 increments) and with five different combination of feature classes: linear only; linear and quadratic; linear, quadratic, and hinge; linear, quadratic, hinge, and product; linear, quadratic, hinge, product, and threshold. For each combination of feature classes and regularization multipliers we calculated the corrected Akaike Information Criteria (AICc) based on Li et al. (2020).

We projected the final model (the one with the lowest AICc value) over the entire study area considering yearly intervals and therefore obtaining 16 maps of potential nesting probability, one for each year going from 2000 to 2015. Only a 1 km strip of coastal habitat was considered to project species probability of presence over the Mediterranean basin. On this final model we calculated the contribution of each environmental/climatic variable using a jackknife approach (Warren and Seifert, 2011).

To evaluate the reliability of our results, we used a repeated split-plot approach with 10 replicates randomly dividing the calibration dataset into a training set (including 80 % of the presence data) and a test set (with the remaining 20 % of nests). For each run

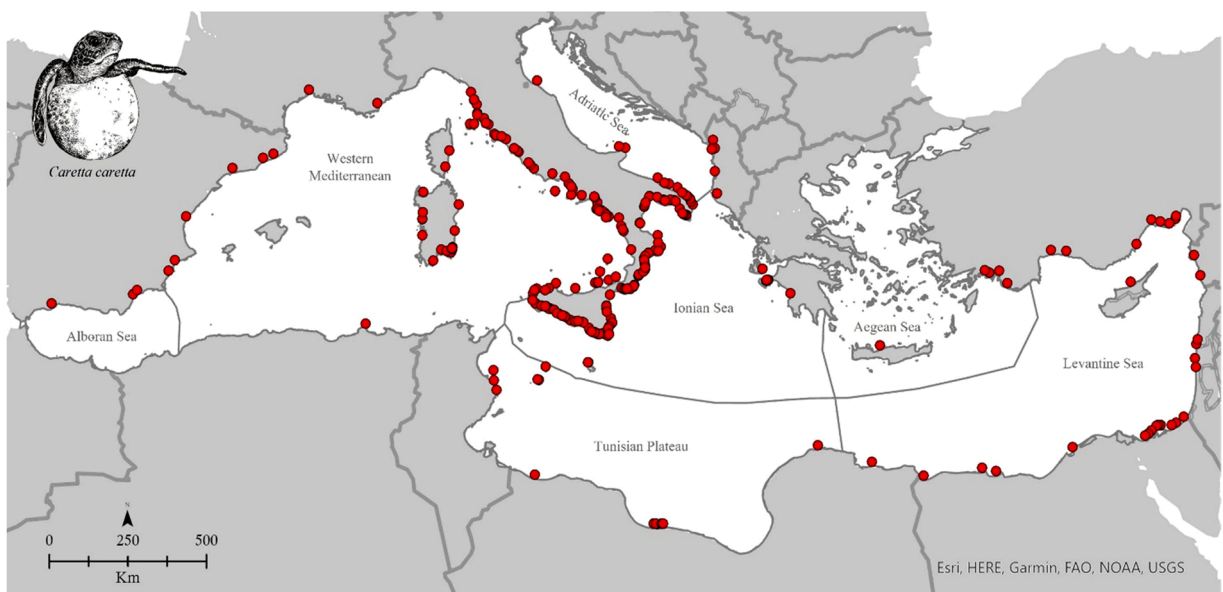


Fig. 1. Nesting locations of *Caretta caretta* in the Mediterranean basin from 1963 to 2020.

we calculated the AUC value (Phillips et al., 2006) and tested its statistical significance following Raes and ter Steege (2007).

For each ecoregion we measured changes from year to year in relative probability of nesting for loggerhead turtles counting changes in probability values on a cell per cell base. To avoid overestimating changes, we measured changes after classifying each model into 5 probability classes using 5 equal intervals between a probability of 0 and a probability of 1.

### 3. Results

We collected 666 nesting locations of loggerhead turtles from 1963 to 2020 in the Mediterranean basin (Fig. 1). We found no temporal trend in the share of research dedicated to loggerhead turtle nesting activities in the scientific literature ( $r = 0.39$ ,  $p = 0.44$ ); therefore, we can exclude a significant impact of sampling bias on our results.

#### 3.1. Changes in nest distribution

We found a clear westward trend in the centers of gravity of the nests over time (Fig. 2). In the 1960s the nests were concentrated in the Aegean Sea and Levantine Sea, with a center of gravity placed to the south-east of Crete. Already in the 1970s, the shift towards west was clear, with the nests occupying Aegean Sea and Levantine Sea plus Ionian Sea and Tunisian Plateau, and with the center of gravity located in the Ionian Sea, 624 Km west of the original point. The trend continued in the years almost linearly (726 km in the 1980s, 520 km in the 1990s, 1189 km in the 2000s) and in the last decade (2010–2020) the center of gravity was located south of the Italian coasts, nearby Sicily, some 1298 km west of the original location. In 2020 at least one turtle nest was registered in all Mediterranean ecoregions.

#### 3.2. Nesting model

The final model (see AICc values in Appendix A in Supplementary Material, Tab. A.2) had a very good predictive power (mean AUC =  $0.919 \pm 0.047$ ;  $p$ -value  $\leq 0.001$ ). Both marine and terrestrial variables influenced the final nesting probability, with sandy coastlines, human population, nighttime lights, and sea surface temperature representing the most important variables (Table 2). As expected, the probability of nesting increased with beach availability and decreased with higher human population densities and nighttime lights (Fig. 3). The effect of SST was also very clear, with probability of nesting increasing with increasing temperatures, up to a maximum probability around 24–25 °C, and then dropping down for higher temperatures (Fig. 3).

The 16 yearly maps of potential nesting probability returned a pattern closely following the results obtained with the centers of gravity, with probability of nesting increasing through years towards the northwest of the Mediterranean basin (see Appendix A in Supplementary Material, Fig. A.1). In 2000 the Western Mediterranean and the Ionian Sea were dominated by areas with low probability of nesting, but the probability increased through time, with 80 % of both seas characterized by areas with high probability of nesting in 2015. The Adriatic Sea, the Levantine Sea, and the Tunisian Plateau remained relatively stable, with 60 % of high probability areas and with a very limited increase in time. Also, the Aegean Sea and (particularly) the Alboran sea remained stable in time, both dominated always by very low nesting probabilities (Fig. 4; see Appendix A in Supplementary Material, Fig. A.2).

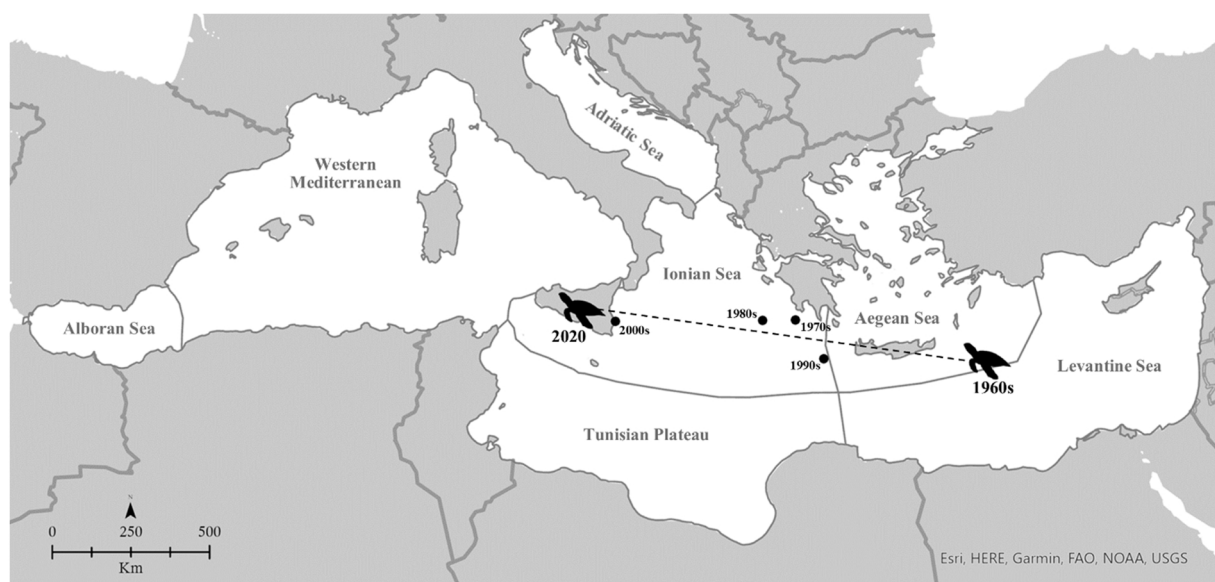


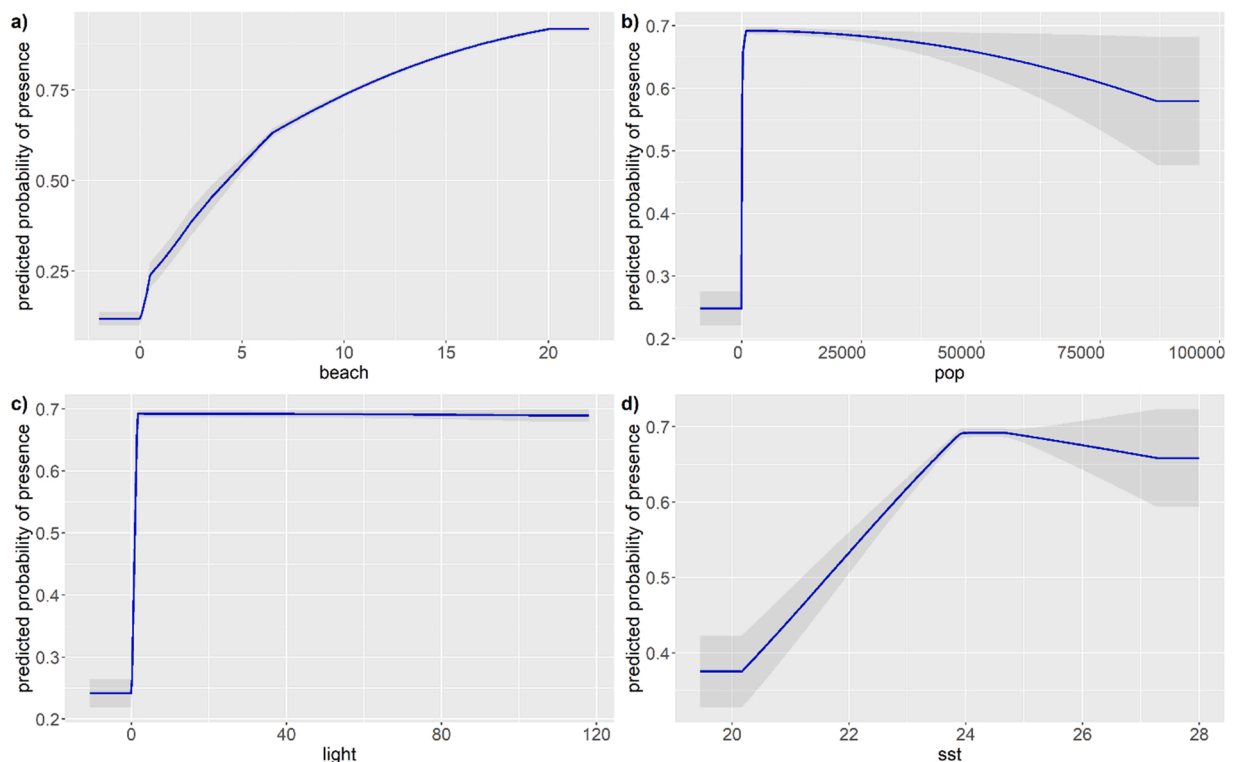
Fig. 2. Decennial centers of gravity of loggerhead sea turtles' nests from 1960s to 2020 in the Mediterranean Sea.



**Table 2**

Contribution of each environmental variable to the final Maxent model. Values shown are averages over 10 replicate runs. Variable names defined as in Table 1.

Variables	Percent contribution
beach	58.2
pop	25.8
light	12.6
sst	2.3
O <sub>2</sub>	0.4
psu	0.3
pH	0.2
chl	0.1
NO <sub>3</sub>	0.1
bathy	0

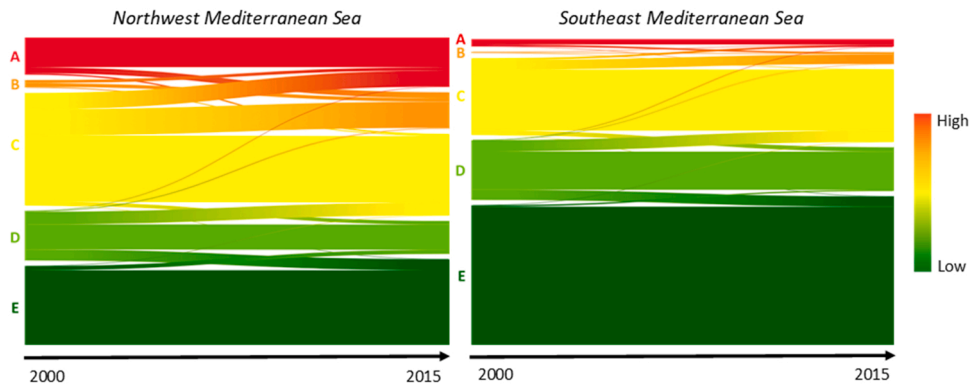


**Fig. 3.** Marginal response curves (mean) for the four most important variables. Shaded areas represent one standard deviation calculated over 10 replicates. Variable names defined as in Table 1.

#### 4. Discussion

Historically, sea turtles were limited to the eastern Mediterranean with most of the nests being recorded in the last 50 years or so in the eastern Mediterranean (Camiñas et al., 2020). Recently, a few authors have proposed that loggerhead turtles are expanding their nesting grounds towards the western Mediterranean basin (Carreras et al., 2018; Girard et al., 2021; Hochscheid et al., 2022). The hypothesis, up until now, has not been tested formally and it could easily be linked to a sampling bias resulting in an apparent range shift. To test this idea, we built a robust database spanning the last 60 years and we measured a sharp and clear pattern, with a net increase in nests along the coasts of the Italian peninsula and with propagules expanding up to France and Spain. Overall, the center of gravity for all nesting grounds shifted roughly of 1300 km to the northwest, corresponding to a range expansion speed of 21.6 km per year.

We performed our analysis considering a database including all nests recorded in peer-reviewed, technical, or grey literature, also including all reliable personal communications that we have been able to collect directly from the sources. While we found no temporal trend in the share of research dedicated to sea turtle nesting over the years, we cannot exclude a priori the fact that a sampling bias is present also in our database, especially for the first years (i.e., from 1960s to late 1980s). It is possible that before 1990s a few isolated



**Fig. 4.** Sankey diagrams of northwest (Western Mediterranean, Ionian Sea, Adriatic Sea, Alboran Sea ecoregions) and southeast (Levantine Sea, Tunisian Plateau, Aegean Sea ecoregions) basin of the Mediterranean Sea. Relative probability of presence was classified into 5 probability classes, ranging from high probability (A; red) to low provability (E; dark green).

nests in the western Mediterranean have been overlooked, especially if placed along the African shores. The net result would be minor in any case. In fact, we analyzed the trend in species distribution considering 10 years intervals, exactly to avoid being influenced by unpredictable year-to-year variations, which could occur both in the sampling and in the actual nesting.

It is important to note that our analyses are based on nest presence, without any explicit consideration for nest densities on single beaches. The number of nests in the eastern basin is overwhelming if compared to those in the west, with over 96 % of nests found in Greece, Turkey, Libya, and Cyprus and with no nesting activities documented (even in recent years) for Algeria, Morocco, Bosnia and Herzegovina, Croatia, Montenegro, and Slovenia (Margaritoulis et al., 2003; Casale, 2010; Casale and Mariani, 2014; Casale et al., 2018, 2020). Measuring a center of gravity based on nest densities would have produced a net change of zero over the years. However, our original research question is focused on changes in distribution range, not on changes in nesting densities.

Using state-of-the-art modelling techniques in a multitemporal calibration approach (*sensu* Maiorano et al., 2013), we demonstrated that the distribution of nesting grounds in the Mediterranean is guided by both marine and terrestrial factors. Our results are in line with what has been found in other parts of the world (e.g., Garçon et al., 2010; Putman et al., 2010; Fuentes et al., 2011). The availability of sandy shores represents a clear prerequisite (ruling out therefore vast areas along north African coasts which are rocky), coupled with a limited impact of human activities. Very important is also SST in front of the nesting beach, confirming what was proposed by Mazaris et al. (2004). We found a very narrow interval of temperatures that defines beaches suitable for nesting, with optimal nesting grounds corresponding to a SST of 25 °C. This value corresponds strikingly well with the results from field studies suggesting that female turtles during the nesting period actively select waters with temperatures around 24–26 °C (Mrosovsky and Yntema, 1980; Sato et al., 1998; Hays et al., 2003).

All these factors explain very well the spatial pattern that we found in nesting probabilities. The Aegean coasts, between Greece and Turkey, are characterized by lower temperatures and by a limited number of beaches, while almost every suitable beach in the Levantine basin (i.e., from Turkey to Egypt) is basically occupied. The western Mediterranean and the Ionian basin see a constantly increasing probability of presence, potentially opening a huge set of nesting grounds for the species. Same pattern, although in a much smaller scale, is occurring in the Adriatic Sea, while the probability of nesting in the Alboran sea, at the westernmost part of the Mediterranean is (and has always been) very low. Incidentally this pattern can also provide an explanation for the genetic isolation between the Mediterranean and the Atlantic populations.

Our results correspond very well with the trends in SST in the Mediterranean, which increased of 1.4 °C from 1978 to 2003 (Rixen et al., 2005; Belkin, 2009). The increase in SST was stronger for the eastern basin (where suitability for nesting ground remained basically stable in time) and weaker for the western basin (respectively 1.01 °C for the first and 0.62 °C for the second; Skliris et al., 2012). In both cases the highest level of warming is concentrated from May to July, exactly during the nesting period for loggerhead turtles in the Mediterranean (Pastor et al., 2019).

In this context, it's important to have a clear picture of the species potential distribution to be able to guide future management and conservation efforts for a highly mobile species expanding its range into a human dominated ecosystem. A coordinated, international effort must be based on large scale knowledge of the species potential distribution. Despite several studies focusing on different aspects of loggerhead turtles' ecology, management, and conservation in the Mediterranean Sea (Casale et al., 2018), we are presenting here for the first time a large-scale model of the potential distribution of nesting grounds for the species in the entire basin. With our multiyear model we have been able to show that loggerhead turtles follow climate change moving outside of the historical nesting areas, towards latitudes and longitudes that become suitable for incubating eggs. This has already happened during the most recent glacial period (18,000–12,000 years ago), when warmer temperatures facilitated the expansion of *Caretta caretta* to higher latitudes (Bowen et al., 1993).

Besides climate (and climate changes), human activities are clearly the main danger for turtles' nesting grounds. Urbanization and development have substantially altered nesting grounds around the world (Herren, 2014; Cope, 2015), and even mild interventions like beach nourishment can negatively impact sea turtles, not so much on nesting but on hatching success. In fact, if the sand is too

compacted or if the sand imported is drastically different from native beach sediments clutch survival may be compromised (Rumbold et al., 2001; Patino-Martinez et al., 2022). Clearly, the most serious threat caused by increased human presence on the beach is the disturbance to nesting females. Night-time human activity can prevent sea turtles from emerging on the beach or even cause females to stop nesting and return to the ocean. Furthermore, hatchlings have an innate instinct that leads them in the brightest direction, which is normally moonlight reflecting off the ocean (Price et al., 2018). Excess lighting from the nearshore buildings and streets can cause hatchlings to become disoriented and wander inland, where they often die of dehydration or predation (Price et al., 2018). While we spotted a clear response in our model to human population density, the ecological interpretation of the response curve for nighttime light is counterintuitive (Fig. 3). We found that probability of presence for a nest is low in the absence of nighttime light, and it increases to a median level as soon as light is present; then it steadily increases at increasing light levels, giving a result that is opposite to what we were expecting. However, the spatial resolution of our data on nighttime light is 1 km<sup>2</sup>, being probably too coarse for a variable whose effect is limited to local areas.

Our modelling approach combine multi-temporal calibration in a multi-realm SDM (Häkkinen et al., 2021) providing a novel avenue for integrating into a single, coordinated, large scale analyses historical biodiversity data for species spanning multiple realms. The loggerhead sea turtle represents a potentially useful flagship species, being highly mobile, spanning two different realms, and catalyzing the attention of the general public. An important research priority is understanding how climate change will influence the location and extent of climatically suitable nesting habitat. Future global changes are expected to occur unprecedented and the survival rates at which the species may be able to cope with the predicted change are uncertain. Sea turtles are part of two ecosystems, the coastal and the marine system. If sea turtles would continue to be threatened by climate change, both the marine and coastal ecosystems would be negatively affected. While the species is not losing suitability in the Eastern basin, we need to focus the limited conservation resources to where actions can produce effective conservation outcomes. In the eastern Mediterranean basin, active beach patrolling and nest control represent probably the most important factor in ensuring the lowest possible mortality for hatchlings, maintaining a population which currently represents (and will represent in the near future) the source for individuals wondering in the entire basin. In the ecoregion of the Ionian Sea and the Western Mediterranean the loggerhead sea turtle can function as the key element to promote a proactive approach, even for beaches/areas where the species is not present with huge numbers of nests, potentially fostering a positive impact on conservation and restoration of coastal areas in the Mediterranean.

### CRediT authorship contribution statement

Focus of the research teams: Chiara Mancino Marine biology, Macroecology and Biodiversity Conservation <https://maioranolab.com/people/lab-members/chiara-mancino/>; Daniele Canestrelli Ecology, Evolution and Conservation biology <http://www.danielecanestrelli.com/>; Luigi Maiorano Macroecology and Biodiversity Conservation <https://maioranolab.com/people/luigi-maiorano/>.

All authors conceived the idea and designed the methodology. Chiara Mancino ran all the analyses and wrote the original first draft. Luigi Maiorano and Daniele Canestrelli supported and contributed to the analyses' methodology. All authors contributed substantially to the writing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02264](https://doi.org/10.1016/j.gecco.2022.e02264).

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