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Nesting range expansion of loggerhead turtles in the Mediterranean: Phenology, spatial distribution, and conservation implications

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ABSTRACT

Global warming is affecting habitat quality and availability on our planet and some species are predicted or are by now changing their distribution range. Here we show that loggerhead turtles have already started to expand their nesting range into the Western Mediterranean, which has until recently hosted only sporadic nests. We compiled information on nesting activity from beaches surrounding the Western Mediterranean and collected metadata on loggerhead turtle nests in Spain, France, Italy, and Tunisia between 2010 and 2020 to provide an exhaustive overview on the phenomenon of emerging new nest sites for loggerhead turtles. The number of recorded nests has increased drastically since 2013 from 1 to 3 nests/year to a record number of 84 registered in 2020. While this increase may partly be explained by grown awareness and reporting by citizens, there is no doubt of an upward trend in nesting activity. The nests are unevenly distributed over the study area with most nests occurring on the coasts of the warmer Tyrrhenian Sea. A hotspot analysis identified beaches in SW Italy, SE Sardinia, and NW Tunisia with statistically significant clustering of nests. Within these hotspots, three beaches in SW Italy and one in Tunisia had nests at least four out of the five last years. Nesting phenology corresponds to that of Eastern Mediterranean rookeries, and mean hatching success of naturally incubating, non-manipulated nests was 66 %, although there was variability across the region. Mean incubation durations also varied between countries indicating a diversity in inferred sex ratios, with sufficient female production to foster future colonisation of this region. Unfortunately, these beaches are already under high tourist pressure and subject to intense coastal development, imposing many threats to the females, eggs, and hatchlings. Thus, while this study reveals the unique opportunity to witness and study an ongoing new colonisation process in loggerhead turtles, it also calls for urgent proactive conservation actions to mitigate these threats and allow the turtles to establish new rookeries.

1. Introduction

An important and well-established adaptive response to climate warming is the re-distribution of species' geographical ranges (Parmesan and Yohe, 2003; Thomas, 2010). The close coupling between thermal tolerance and environmental temperature leads marine species, especially ectotherms, to shift their boundaries towards poleward latitudes (Sunday et al., 2012). Sea turtles, a conspicuous group of large marine ectotherms, are tied to temperature regimes both on land, where they lay their eggs, and in the oceans, where they develop, forage, and mate. Therefore, it can be expected that foraging and nesting range expansions are uncoupled in sea turtles because the shifts in isotherms are different in terrestrial and marine environments and act differently on sea turtles' life history traits. Moreover, the interplay of some traits, such as ontogenetic habitat shifts, long distance migrations, natal philopatry, and temperature dependent sex determination (TSD), make sea turtles unique models for studying and assessing the impact of climate change, a threat that is still poorly understood despite the increased attention of policy makers, scientists, and the general public (Rees et al., 2016; Patrício et al., 2021).

The circumglobal distribution of nest sites for most sea turtle species is proof that colonisation of new habitats has been made possible over the 120 million years of evolutionary history of sea turtles, even across ocean basins, by wandering and exploring females or those that nest opportunistically in the vicinity of their foraging areas (Jensen et al., 2013; Carreras et al., 2018). As the present geographical distribution of sea turtles demonstrates, the range expansion potential of the species has been sufficient to match past environmental changes (Carreras et al., 2018). Unfortunately, current climate change and coastal development are happening at much faster rates, and conservationists and researchers alike fear that sea turtles will not be able to adapt and respond fast enough (Tanner et al., 2019; Fuentes et al., 2020; Patrício et al., 2021). In fact, some ocean regions, including the Mediterranean Sea, have already warmed >1–2 °C over the past 25 years (Pastor et al., 2018), which is less than a generation of sea turtles and just about the time that it takes for hatchlings to grow into adults and start nesting. Given the TSD of sea turtles, such a change in temperature is predicted to have profound effects on primary sex ratios, leading to the feminization of sea turtle populations (Glen and Mrosovsky, 2004; Hawkes et al., 2009; Jensen et al., 2018; Monsinjon et al., 2019). On the other hand, hatchlings returning to their natal beaches to nest for the first time may not even find these beaches anymore, due to massive constructions (e.g., for tourism, urbanisation, ports, and industry), that in turn may lead to erosion of these beaches (Lopez et al., 2015).

In the context of colonisation and environmental change, the loggerhead turtle in the Mediterranean Sea is an interesting case study. Here, the loggerhead turtle is the most widely distributed sea turtle species, with foraging habitats in most marine areas and the biggest nesting colonies in Greece, Turkey, Cyprus, and Libya where the busiest beaches host between 53 and 222 nests $km^{-1}y^{-1}$ (Margaritoulis et al., 2003; Margaritoulis, 2005; Casale et al., 2018; SPA/RAC-UNEP/MAP, 2021). Loggerhead turtles from the Atlantic have colonized the central and eastern Mediterranean Sea in at least two independent events in the late Pleistocene and the Holocene (Garofalo et al., 2009; Clusa et al., 2013). Although Atlantic loggerhead turtles still enter the Mediterranean to forage, they do not usually reproduce there (but see also Carreras et al., 2018). Instead, they leave the Mediterranean at large juvenile stages when they are strong enough to swim against the strong surface currents in the Strait of Gibraltar (Revelles et al., 2007; Eckert et al., 2008).

Genetic structuring because of the natal philopatry of loggerhead turtles has differentiated the Mediterranean sub-population from the Atlantic ones (Carreras et al., 2011; Shamblin et al., 2014), forming an independent Regional Management Unit (RMU) (Wallace et al., 2010). The most recent IUCN Red List assessment of the status of the Mediterranean loggerhead RMU resulted in a "downgrading" to the threat category "least concern" due to the increasing trends in eastern Mediterranean nesting rookeries (Casale, 2015). This new status classification tells a success story for over 30 years of conservation projects on the major rookeries in Greece, Turkey and Cyprus. However, major threats persist and have not been found to decline, so that the Marine Turtle Specialist Group of the IUCN Species Survival Commission released a statement that the "least concern" RMU's are "entirely conservation-dependent and any decrease of the current conservation effort would very likely be detrimental for these subpopulations". Now, it must be said that the population trend analyses were based on long-term data sets available from 16 rookeries in Greece, Turkey, Cyprus, and Israel, whereas no sufficient data were available from the other habitual nesting areas, all located in the Eastern Mediterranean such as Libya, where recent monitoring programmes report nesting densities of up to 100 nests/km (SPA/RAC-UNEP/MAP, 2021). Hence, the actual number of just under 10,000 nesting females may likely be underestimated.

While these figures are being updated for the Eastern Mediterranean, a new situation is arising in the Western Mediterranean. This basin, which connects to the eastern part only through the small Strait of Messina and the Sicily Channel, has only ever hosted occasional loggerhead turtle nests (Casale et al., 2018). On Spain's coasts, sporadic unclear records of nesting evidence have been quoted in the literature until a first nest was confirmed in 2001 (Tomás et al., 2002). The following year, Italy and France reported their first nests. Since then, other sporadic nesting events have been recorded on the Western Mediterranean coasts (Tomas et al., 2008; Bentivegna et al., 2010; Bradai and Karaa, 2017) including reports on the "northern-most" and "western-most" nests (Sénégas et al., 2008; González-Paredes et al., 2021). Nesting activity seems to be increasing, although still in low numbers, and has assumed regular character in some regions (Maffucci et al., 2016). A recent genetic study on the nests from these countries made a case for long-distance colonisation since several of the clutches in Spain could even be assigned to Atlantic parents (Carreras et al., 2018). Naturally, the increasing reports on nests in the Western Mediterranean have given rise to speculations on the possible reasons for this observed change in behaviour. Based on the monthly time series of sea surface temperatures in the Tyrrhenian Sea over the past 60 years, Maffucci et al. (2016) associated a trend of steadily warming temperatures, especially over the last years, to the increase in the number of nests in southwest Italy. Climate warming can provide turtles with the opportunity to form new colonies as new habitats become available that were previously too cold for the incubation of sea turtle embryos (Witt et al., 2010; Pike, 2013b). Usually, as mentioned above, range expansion is a slow process, however rapid population growth stemming from historic or contemporary conservation efforts may lead to the spatial "spillover" effect, and hence to an increase in the frequency of exploratory animals (Pike, (2013b) and references cited therein).

Whatever the reason, today's nesting in the Western Mediterranean has become regular, at least in some areas. Unfortunately for these nesting turtles, the beaches here have long been frequented and exploited by humans, and Spain, France, and Italy are among the top seven countries with the highest tourist pressure on Mediterranean coasts (UNEP/MAP, 2012). Hence, the emerging nesting sites are facing many threats, which could hamper new colonisations or even preclude them altogether (Geringny et al., 2016). Here, with the aim to summarise and show the development of loggerhead nesting on the Western Mediterranean coasts over the past ten years, we have collected all data available from France, Italy, Spain, and Tunisia. We intended to analyse the spatial distribution and trends of sea turtle nests and deliver the first reproductive parameters for this emerging nesting area. Furthermore, we evaluated the impact of public awareness for the monitoring and discovery of turtle nests, as well as the anthropogenic impact on the nesting habitat, and ultimately, hatching success, and the conservation management strategies to mitigate these threats.

With this detailed analysis of nesting data, we discuss the case study of the Western Mediterranean as the beginning of a range expansion of the loggerhead turtle into a habitat already heavily used by humans, and hence the need for proactive conservation measures.

2. Materials and methods

2.1. Records of sea turtle nesting activity

A database was created containing information on loggerhead turtle nests in the Western Mediterranean between 2010 and 2020. Researchers studying nesting turtles in France, Italy, Spain, and Tunisia were asked to insert all available information on confirmed nesting events during this period in their respective countries into the database. The requested information can be derived from the column titles in the Suppl. Table S1. Definitions and explanations for each requested information was also provided to the contributors and can be accessed in Table S2.

We acquired additional information from other published sources on nests that occurred in the study region but for which no data were available to the contributing authors. Data on these nests were also added to Table S1 and were only used to produce the distribution map and to provide total numbers of nest counts, since other metadata were not available.

Nesting attempts were also registered in Spain, France, and Italy. These included tracks left on the beach by a female for which no nest could be identified during expert inspection, or where the female was observed, but abandoned the beach without laying eggs. Although these data were not available for the whole study area, we included records on nesting attempts since many females abandoned the nest site because they were disturbed by the presence of people on the beach. This information was considered important to evaluate the impact of tourism and coastal development on sea turtle nesting on Western Mediterranean beaches.

Since information on most sea turtle activities (either nesting or attempts) heavily rely on the alertness of citizens, with the few exceptions where beach monitoring was carried out (see "beach monitoring"), the tracks with or without nests have likely the same probability of being reported. We are thus confident that the number of nesting attempts recorded in this review are as representative

Table 1
Monitoring carried out on some Italian beaches to detect sea turtle tracks and record nesting activity. All beaches (sections) were monitored 100 %.

Beach name	Region	Beach length (km)	Period (dd/m)	Year (s)	Western limit (LAT, LON)		Eastern Limit (LAT, LON)		Monitoring level	Monitoring protocol	Nests detected*
Acciaroli	Campania	1.8	15/6–31/7	2020	40.1831	15.0245	40.1952	15.0178	Level 2	Protocol B	0
Baia Arena	Campania	1.1	15/6–31/7	2020	40.2333	14.9521	40.2286	14.9622	Level 2	Protocol B	0
Marina di Eboli	Campania	13.1	15/6–31/7	2020	40.5793	14.8837	40.4829	14.9435	Level 1	Protocol B	1
Marina di Capaccio	Campania	2.4	15/6–31/7	2020	40.4605	14.9571	40.4770	14.9468	Level 1	Protocol B	0
Ascea	Campania	5.1	15/6–31/7	2017, 2020	40.1252	15.1802	40.1627	15.1438	Level 1	Protocol B	0/5
Palinuro-Pisciotta	Campania	3.2	15/6–31/7	2010, 2017, 2020	40.0467	15.2840	40.0736	15.2722	Level 1	Protocol B	0/2/0
Camerota	Campania	3.8	15/6–31/7	2010, 2017, 2020	40.0321	15.3102	40.0075	15.3399	Level 1	Protocol B	0/0/1
Riva del Sole	Tuscany	4.5	1/6–31/8	2019, 2020	42.7765	10.7938	42.7660	10.8613	Level 1	Protocol B	1/1
Rimigliano	Tuscany	5.5	1/6–31/8	2020	43.0165	10.5192	43.0633	10.5339	Level 1	Protocol B	1
Le Marze	Tuscany	10	1/6–31/8	2019, 2020	42.7609	10.8825	42.7149	10.9813	Level 1	Protocol B	1/0

[*] Separated by "/" for different years.

for overall nesting activities in the study area as are the actual nests themselves.

2.2. Beach monitoring

Because of the sporadic nature of loggerhead nesting activity in the Western Mediterranean, beaches were never monitored until recently when a few years of nest records gave first indications of beaches where nesting probability was such that a beach monitoring might discover tracks. However, due to the widely dispersed nesting activities, systematic monitoring protocols could not always be applied. Here we report for each of the three countries how the monitoring was organized and carried out.

In Italy, beach patrols were carried out either on foot or, for longer stretches, by e-bike in the early morning to discover and locate tracks left by the females. These were the only beaches for which the monitoring effort could be classified following the protocols and levels described by (SWOT, 2011) (Table 1). Occasional monitoring was carried out with the aid of unmanned aerial vehicles (UAV) over 10–15 km stretches of beach in the Calabria region (SW Italy). However, this monitoring was carried out only the day after a nesting attempt was reported to verify if and where the female re-emerged to lay eggs.

In Spain, after the discovery of a nest in the Valencia province in 2006 (Tomas et al., 2008), irregular beach patrols were carried out by technicians of the regional government during 2007. Early morning monitoring of beaches were made by volunteers in several stretches of coasts in the regions of Andalucía (36.7°N-3.4°E), Murcia (38.0°N–1.5°E), Valencia (39.5°N–0.75°E) and Catalonia (41.82°N–1.87°E) since 2017.

In France, the NGO CESTMed initiated in 2017 a survey of Regional Nature Park of the Camargue (43.55°N–4.57°E) beaches from June to September, monitored by volunteers on foot or by beach operators before cleaning the beach in the morning. The monitoring continued until 2021, covering a combined total length of 122.1 km of surveyed beaches.

2.3. Management of nests and hatchlings

All contributing authors were also required to provide general information on management measures that were adopted for each nest and the emerging hatchlings, and to provide more specific details if a particular procedure was not contemplated in the database. This information is also defined in Table S2.

The relocation of nests was registered as a Yes/No response. Usually, nests are relocated when they are too close to the water and risk inundation, but also when a nest is judged to be in an "unsafe" position and at any risk if left in place. There are standard procedures available for this operation and most experts follow these and act based on their own experience. This is not the place to describe nest relocation in detail, but readers may refer to, for example, the recently published "Marine Turtles in MPAs: a Monitoring and Management Guide for MPAs" (Rees, 2020). In each country, the relocation of a clutch or part of a clutch was always carried out by experienced and trained scientific operators.

In Spain, many clutches were dug out and split in two parts, relocating one part to another position on the beach or to another beach entirely (approximately 2/3 of the clutch), and the other part was placed into artificial incubators at marine turtle rescue centres of the same region in which the clutch was laid following procedures described in LIFE Intemares (2020). Incubation temperature of the incubators was usually set initially to values of pivotal temperatures estimated for the species in the eastern Mediterranean (29.3 °C (Mrosovsky et al., 2002) or slightly higher (29.5 °C)), and then increased weekly during the last third of the incubation period until 31 °C to imitate metabolic heating of eggs and to ensure female production.

In France, one nest (FR_01, 2016, Table S1) was relocated to an artificial incubator towards the end of the incubation period according to the method used in French Guiana (Jacques Fretey, pers. com.). However, afterwards it was collectively decided not to interfere with the natural nesting process anymore, and to only collect data and samples to document the viability of nests along with the climate changes.

Clutch size, hatching and emergence success, and hatchling measurements.

Clutch size, hatching (HS) and emergence success (ES) were determined after commonly used procedures following Miller et al. (1999). For some nests (38 of 175 nests), hatchling dimensions (straight carapace length [SCL] and straight carapace width [SCW]) were measured with a calliper to the nearest millimetre, and body mass was measured to the nearest decimal gram.

2.4. Threats and anthropogenic impact

Threats to loggerhead turtle nests on Western Mediterranean beaches were assessed by indicating whether a nest was predated or inundated, and by selecting a general level of anthropogenic impact and the level of light pollution at the nest site. Anthropogenic impact levels were distinguished between "pristine", "low", "medium", and "high" as defined in Table S2. Beachfront lighting on the nesting sites was assessed by three ranks (0, 1, or 2), also defined in Table S2, whereas the ranking was modified from Varela-Acevedo et al. (2009).

2.5. Statistical analysis and mapping

Not all requested data were available for all nests and/or countries, therefore the sample sizes in statistical summaries varies accordingly for these values. Mean hatching and emergence success were obtained by dividing the total number of hatchlings that hatched and emerged, respectively, by the total number of eggs. The software Minitab® 17.1.0 was used for the analysis and graphics, except for the spatial analysis described below.

To investigate the spatial pattern in loggerhead turtle nesting, an evenly spaced grid with 15 × 15 kilometres cells, was placed over the Western Mediterranean coastline in QGIS 3.18.1 software. The Hotspot Analysis Plugin was employed to compute Z-scores and relative p-values of the Getis-Ord Gi* local statistics (Ord and Getis, 1995) to identify areas with statistically significant clustering (local autocorrelation) in the spatial pattern of loggerhead turtle nesting (Oxoli et al., 2017). Hotspots, i.e., higher number of nests than expected by chance alone, were identified as those locations with Z values >2 and associated p-value <0.05.

Within the statistically significant clusters identified by the hot spot analysis, we searched for those beaches where loggerhead turtle nests have been found at least four years out of the last five. Only for these locations did we calculate the number of nests/km/year.

3. Results

3.1. Records of sea turtle nesting activity

Overall, 206 loggerhead turtle nests were found on Western Mediterranean beaches between 2010 and 2020, including nests found through literature search in Algeria (N = 1) and Italy (N = 25). The total number of nests for which the authors of this study provided more detailed information was 175, with contributions from France (n = 5), Italy (n = 126), Spain (n = 29), and Tunisia (n = 15) (see Table S1).

To provide a better overview of overall nesting effort in the region, we also considered data on nests < 2010 that have already been published (N = 13, Table S1 and references cited therein) to produce Figs. 1 and 2a. Loggerhead turtle nests in the Western Mediterranean were sporadically reported (~ 1 yr^{-1}) during the first decade of this century and then numbers increased steadily since 2012, reaching a record number of 84 in 2020 with more than three times as many nests as registered in the years before (Fig. 1). There was a strong correlation between year and nest number (Spearman rho for year and N nests = 0.854, $P < 0.0001$), but we refrained from any trend analysis in the time series data since the methods for recording nest numbers were mostly not coherent with the minimum data standards for sea turtle nesting beach monitoring (SWOT, 2011).

Nests were unevenly distributed along the Western Mediterranean beaches, with most nests occurring on the Tyrrhenian coasts of mainland Italy, Sardinia, and northern Sicily followed by a number of nests scattered along the coasts of Spain including the Balearic Islands (Fig. 2). There were only a few nests recorded on French Mediterranean coasts and Western Sardinia, and no nests on the coasts of the Ligurian Sea. For the North African coasts, there were no reports of nesting activity apart from the nests registered in Tunisia and the one record in Algeria. Overall, there were fewer nests at western longitudes, but with higher occurrence at northern latitudes (e.g., more nests in northern Spain, none on North African coast) and there were more nests at eastern longitudes with a higher occurrence at southern latitudes (e.g., more nests in SW Italy and SE Sardinia), Specifically, the Cilento Park in the Campania region of SW Italy received 32 % of all recorded nests in the Western Mediterranean and is the only area which registered more than 20 nests (with a maximum of 29) per cell of 15 × 15 km. The hotspot analysis confirmed the Cilento beaches had statistically significant clustering of nests, but also identified hotspots around the Capo Carbonara Marine Protected Area in southeast Sardinia and in the Nefza area in northwest Tunisia (Fig. 2b).

Within these hotspots, only four beaches had nests regularly identified at least four out of the five last years, three in the Cilento Park and one in Tunisia (Table 2).

The nesting season in the Western Mediterranean lasted on average 118 days, comprising the months of June to August for nesting, and July to October for hatchlings' emergence. Over the region and study period, the earliest nesting occurred on the 5th of June in 2020, and the latest date for a nest was 31st of August 2014. The earliest date for a nest to hatch was on 15th of July 2014 and the latest date of hatching was on 31st of October 2016. Table 3 summarizes the principal parameters of loggerhead turtle nests in the Western

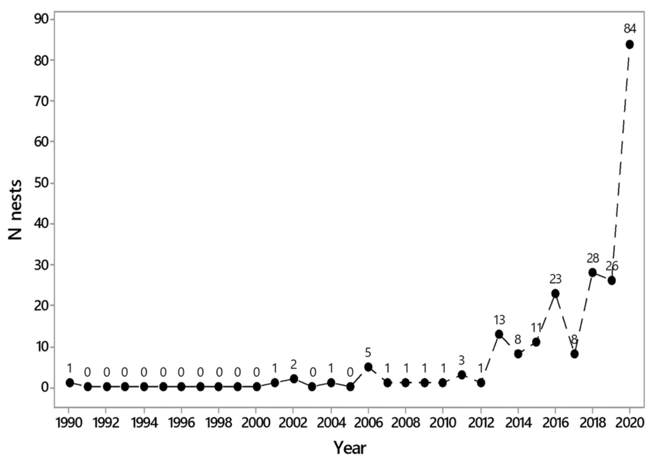

Fig. 1. Number of loggerhead turtle nests recorded per year in the Western Mediterranean in the years 1990–2020 (N = 219).

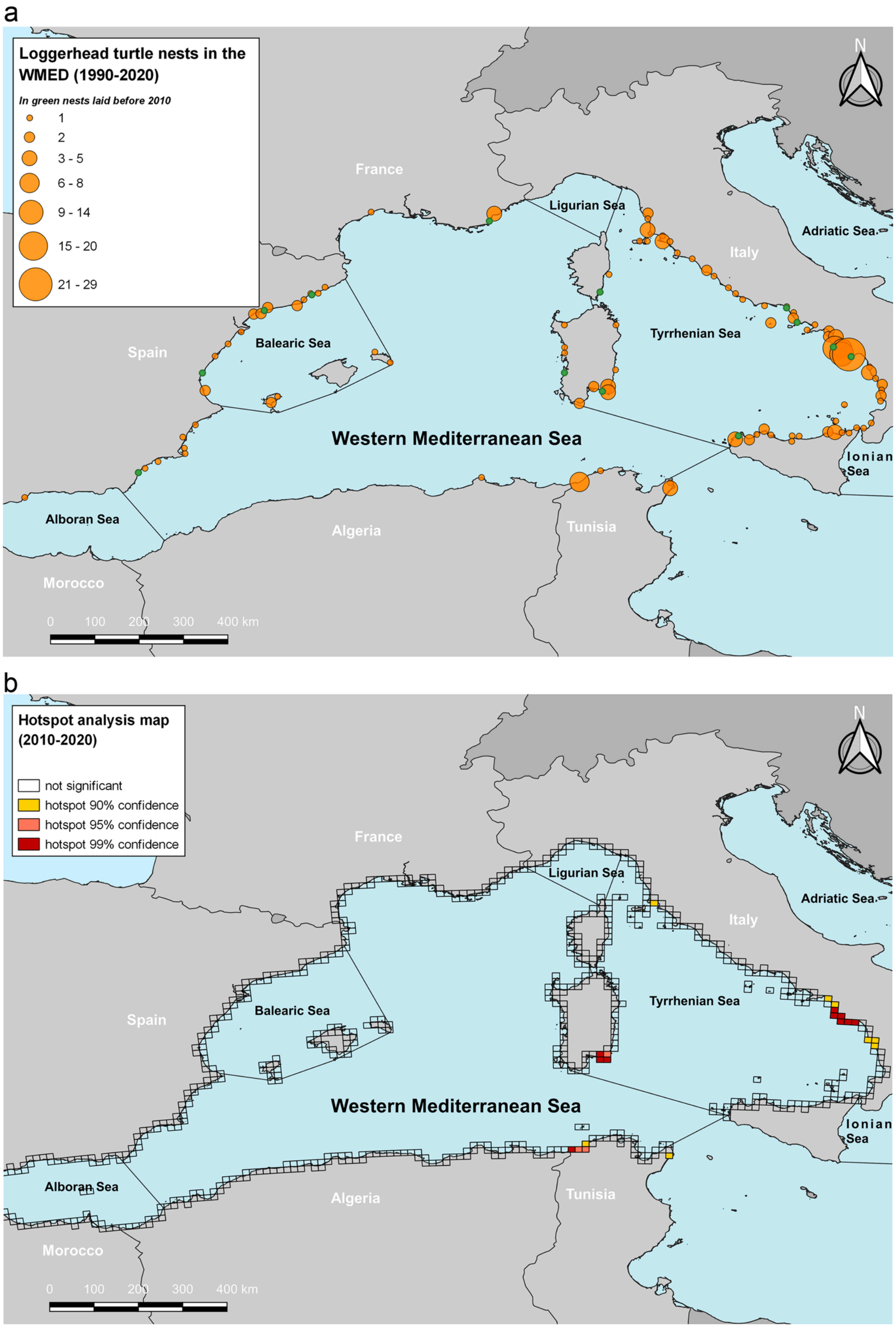

Fig. 2. Distribution of loggerhead turtle nests in the Western Mediterranean; a) number of nests per 15 km, symbol size increases in proportion with number, green dots indicate single nests registered before 2010; b) hotspots for nesting in the Western Mediterranean, see details in methods for how the hotspot analysis was performed. Solid lines indicate borders of sea regions.

Mediterranean.

A total of 120 nesting attempts were registered: eight in France, 74 in Italy and 46 on Spanish beaches (Table S3). While in the years 2010–2013 there were only few activities registered overall, after 2014 there were proportionally more nesting attempts in Spain than in Italy (Likelihood Ratio Chi-Square = 19.816; DF = 1; $P \leq 0.001$). Data for France were not included in this analysis due to the small sample size. Reports of tourists and citizens on the beach that disturb the female turtles while they are trying to nest are common

Table 2
Nesting density of 4 beaches identified in the hotspot analysis which had regular nesting activity over the past 5 years. In bold values that equal the threshold of nest density of major nesting beaches defined by Casale et al. (2018).

Country	Beach name	total nests	N Nests/km/year				
			2016	2017	2018	2019	2020
Tunisia	Chott Zouaraa	8	0.07	0.07	0.00	0.13	0.27
Italy	Acciaroli/San Mauro	9	0.50	0.50	0.00	0.50	**3.00**
Italy	Ascea - Scogliera	13	0.50	0.00	0.50	2.50	**3.00**
Italy	Palinuro - Le Saline	15	1.67	0.67	1.00	0.00	1.67

Table 3
Summary statistics for reproductive parameters of loggerhead turtle nests in the Western Mediterranean. ES = Emergence success, HS = Hatching success. ES and HS are reported separately for nests that were left in the original location (natural) and nests that were relocated (not including those transferred to artificial incubators).

Country	Clutch size			Incubation duration				ES [%]			HS [%]		
	Mean±SE	Min-Max	N	Mean±SE	Min-Max	N		Mean	Min-Max	N	Mean	Min-Max	N
France	83 ± 14.3	33–120	5	64 ± 9	46–73	3	Natural	60.2	30–66	3	60.1	36.7–68.0	2
Italy	92 ± 2.2	18–160	108	53.1 ± 0.1	42–73	65		64.5	0–97.9	54	73.0	0–95.5	50
Spain	98 ± 5.5	58–173	26	56.2 ± 1.5	44–69	17		64.1	8.6–82.5	7	62.3	8.6–82.5	6
Tunisia	132 ± 6.5	125–138	2	*	*	0		34.8	19.2–49	2	35.4	19.2–50	2
Overall	93 ± 2	18–173	141	54.1 ± 0.8	42–73	85		63.1	0–97.9	66	66.0	0–97.9	60
Italy							Relocated	56.5	0–90.4	29	61.0	0–97.3	29
Spain								45.6	0–93.3	11	45.9	0–93.3	11
Overall								53.4	0–93.3	40	56.6	0–97.3	40

for France, Italy, and Spain. The females often abandon the beach without successfully nesting, either due to disturbance by people, obstacles, or artificial light sources (Fig. S1). These females were often not resighted after an attempt, so it was not always clear where she finally nested.

3.2. Nest detection and beach monitoring

Most nests (65 %) were detected because private citizens (n = 113) reported the presence of females or hatchlings or their tracks on the beach. Also, beach operators (n = 22), including lifeguards, contributed to the discovery of nests, although at a much lower proportion (13 %) which equalled the percent of nests that were found through direct monitoring of the beaches (n = 23). The remaining 17 nests were detected thanks to the reporting of fishermen (n = 9), guards (n = 5), and collaborators (n = 3). A first monitoring project between 2008 and 2010 on selected beaches in the Campania region of SW Italy resulted in no nest detection. In more recent years, monitoring was repeated and extended to other areas and a few nests were detected as a result, predominantly in 2019 (n = 4 nest detections) and 2020 (n = 14 nest detections) and with less success in 2016 (n = 1) and 2017 (n = 2).

3.3. Management of nests and hatchlings

Management and protection measures were not applied consistently. Sixty-nine (39.4 %) of the nests were not protected in any way, while 100 nests were reported to have been protected either by caging against predators (N = 2, 1.1 %), fence against trespassers (N = 5, 2.3 %), 24-h surveys during the entire incubation period (N = 5, 2.9 %) or a combination of these measures (N = 74, 42.3 %). Fourteen nests were protected but it was not specified which protection method was applied.

Translocation of a nest to another position on the same beach or a different beach was adopted as a management measure for 30.5 % (N = 53) nests. In addition, seven clutches from Spain, one from Italy and one from France were transferred into artificial incubators.

Data regarding the assistance to emerging hatchlings were not complete. In fact, for 43 % of the nests (N = 73) no information was provided on how the hatchlings entered the sea. From 22 % (N = 38) of the nests, hatchlings emerged and entered the sea unassisted. For the hatchlings of 14 % (N = 25) of the nests, assistance was provided usually by releasing them into a shaded corridor leading to the sea, which protected the hatchlings from spectators and artificial light sources. A variable number of hatchlings from 10 % (N = 17) of the nests, all from Spain, were head-started, including hatchlings resulting from artificial incubators. For the remainder of the nests (N = 19), a mixture of multiple management procedures and natural release was applied.

Some nests that were not identified at deposition were located through the detection of hatchlings or their tracks on the beach. However, when undetected nests were laid in highly impacted and light polluted beaches, all hatchlings/tracks were found under gangways, under beach club terraces, in parking areas, and on the street or in residences on the back of the beach (Fig. S2). Hence, all the emerging hatchlings crawled towards the most intense light source and did not find the sea on their own.

3.4. Clutch size, hatching and emergence success, and hatchling measurements

Overall mean HS and ES of undisturbed (i.e., not relocated, not predated, and not inundated) nests were 66 % and 61.3 %, respectively (Table 3). Nests that were relocated (but excluding predated and inundated nests) had overall slightly lower mean HS (56.6 %) and mean ES (53.4 %) (Table 3), however, reasons and procedures for relocation were not consistent over the study area, which could have introduced considerable bias so that we refrained from any further analysis of differences in HS or ES between natural and relocated nests. Clutch size was weakly negatively correlated with the day of egg laying (LSR $r^2 = 0.157$, $F = 18.56$, $DF = 1101$, $p < 0.001$) (Fig. 3). Mean hatchling sizes (straight carapace length, SCL) and body masses were gathered from 38 and 33 clutches, respectively. Hatchlings ranged from 3.7 to 4.4 cm in size (mean of mean SCLs = 4.05 cm) and weighed on average between 10 and 17.9 g (mean of means 14.4 g) and were thus within the ranges reported from other Mediterranean nesting beaches (Table 4).

3.5. Threats and anthropogenic impact

There were differences in the level of anthropogenic impact reported for the nesting beaches of the various countries (Fig. 4). Over 80 % of the nests in Spain were found on highly used beaches, whereas none of the nests were made in pristine beach conditions. In fact, nests were generally not found on pristine beaches in the whole study area, apart from three nests in Italy. Overall, more than half of the nests (53.7 %) were located on beaches with high anthropogenic impact (i.e., inside beach clubs or leisure facilities built on the beaches), 32.6 % were on beaches with medium impact, and 12 % on beaches with low impact. Only 1.7 % of the nests were reported for pristine beaches without any regular frequentation of tourists or citizens.

As could be expected, according to the levels of anthropogenic impact, the majority of nests (N = 82, 49.4 %) were located on sites with high light pollution (level 2 - direct artificial light), 63 (38 %) nests were on sites with level 1 (indirect artificial light), and only 24 nests (14.5 %) were made on sites where no artificial light was present.

With respect to natural threats, only eight (4.6 %) nests of 175 were predated, while the majority (n = 153) of the nests were not predated, and the remaining 14 nests had no information provided. Inundation was reported for 20 (11.4 %) of the nest, whereas 138 nests (78.9 %) were not inundated, and no information was available for 17 nests (9.7 %).

4. Discussion

Today, coastal and marine habitats are changing rapidly as a result of CO_2 emission, over-exploitation of marine resources, coastal development, tourism, pollution, insufficient waste management, and climate warming. This puts a lot of pressure on marine biodiversity, especially those species that have lower capacities to deal with these changes, hence leaving them with the choices to either adapt or move away. Indeed, one of the consequences are shifts in geospatial distributions of the species which expand their ranges to habitats more favourable for their development and reproduction (Parmesan and Yohe, 2003). Sea turtles, which have already faced threatening population declines caused by these unsustainable human activities, have shown resilience to important climatic changes, and are capable of long-distance colonisation of habitats that become favourable for embryonic and juvenile development (Jensen et al., 2013). Here we have presented evidence that the loggerhead turtle in the Mediterranean, a sea that is characterised by high

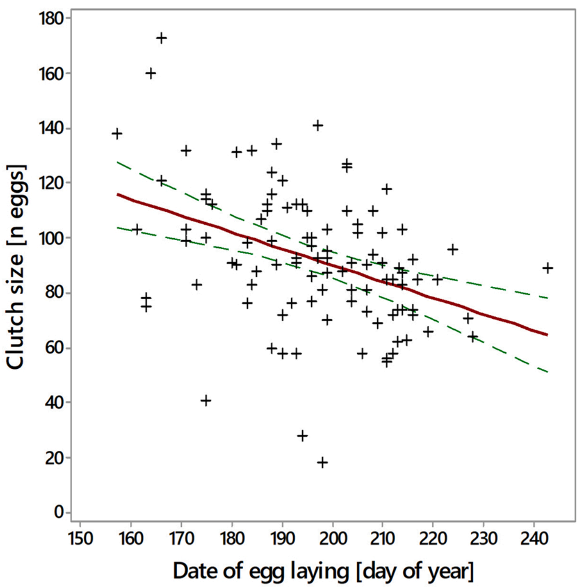

Fig. 3. Correlation between clutch size and date of egg laying (as day of year - DoY). Red solid line = fitted line for least square regression: Clutch size = 209.2–0.5954 DoY egg laying; Green dashed line = 95 % confidence bands.

Table 4
Statistical summary of mean hatchling straight carapace length (SCL) and mean body mass (M_b) which were available for clutches from France (FR), Italy (IT), and Spain (ES). Note: the weighted mean was obtained from mean SCL and M_b, respectively, of each clutch for which mean±SD and number of hatchlings that were measured were available (see data in Table S1).

Variable	Country	N nests	N hatchlings	Weighted Mean	Minimum	Maximum
Mean SCL (cm)	ES	17	414	4.0	3.72	4.28
	FR	3	15	3.9	3.71	4.0
	IT	24	417	4.02	3.6	4.65
	overall	44		4.045	3.6	4.65
Mean M_b (g)	ES	15	365	14.65	13.62	17.94
	FR	4	21	12.68	10.3	14.5
	IT	18	580	14.93	13	16.2
	overall	37		14.78	10.3	17.94

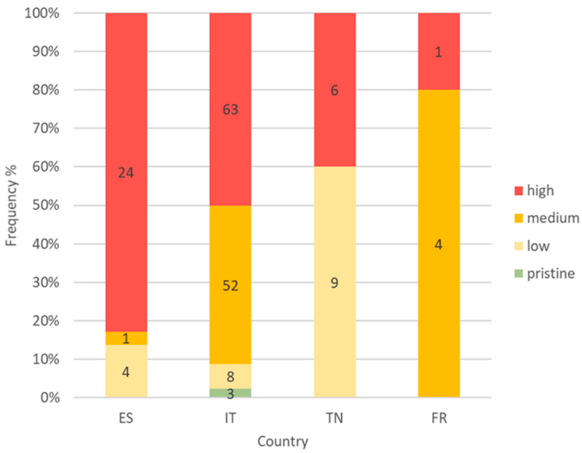

Fig. 4. Level of anthropogenic impact on the beaches where loggerhead turtle nests occurred in the Western Mediterranean, shown for each country separately. Numbers are total counts of nests for each category, zero values are not shown. For description of levels, see Table S2.

coastal population and tourist densities, rapidly warming temperatures, and increasing amounts of marine litter (Suaria and Aliani, 2014), is on the brink of expanding its nesting range.

Until recently, nesting activity by loggerhead turtles was known to be only sporadic in the Western Mediterranean, where females showed no preference of a specific area or beach and nesting was not predictable (Casale and Margaritoulis, 2010; Casale et al., 2018). However, the number of nests has increased rapidly over the last decade, indicating that nests cannot be accounted for by a few stray females, but that the number of females nesting in the western basin has increased. It is not clear yet where these females come from, but genetic studies are underway and will soon shed light on this. A first study by Carreras et al. (2018) had isolated haplotypes characteristic to Atlantic nesting populations from clutches predominantly laid in Spain, but also on other Western Mediterranean beaches. Hence, there is proof of first attempts of long-distance colonisation. Moreover, they reason that "sporadic nesting nearby developmental feeding areas could act as a dormant mechanism of colonisation that activates when the environmental conditions change" (Carreras et al., 2018). Indeed, the Western Mediterranean is known to host developmental habitats where loggerhead turtles originating from Atlantic and Mediterranean rookeries meet and grow together (Carreras et al., 2006; Garofalo et al., 2013; Maffucci et al., 2013; Clusa et al., 2014).

Yet, Western Mediterranean foraging areas are much less frequented by adult turtles than by juveniles (Cardona and Hays, 2017; Casale et al., 2018). The presence of adult turtles in some sea regions may explain the observed heterogeneous distribution of nests in our study area, where most of the nests occurred on beaches bordering the Tyrrhenian Sea. In fact, this sea was recently identified as an important oceanic foraging area for adult-sized loggerhead turtles (Luschi et al., 2018; Chimienti et al., 2020). The Spanish waters instead, are more known as developmental habitats for juvenile turtles (Cardona et al., 2005; Casale et al., 2018), although more recent encounters of adult turtles in Spanish and French waters (Almpanidou et al., 2021; Girard et al., 2021) suggest that they may be more abundant than previously thought. Climate change may further foster re-distribution of adult loggerhead turtles into Western Mediterranean foraging habitats (Chatzimentor et al., 2021). On some rare occasions, females that nested on eastern Mediterranean rookeries in Zakynthos (Greece) and Cyprus were satellite tracked into the Western Mediterranean (Zbinden et al., 2011; Schofield et al., 2013; Haywood et al., 2020), so it may even be possible that they explore opportunistically nearby beaches for nesting in successive seasons. Until today no quantitative assessment of adult loggerhead turtles in the Western Mediterranean Sea is available to support the hypothesis that the distribution of nests is correlated with the distribution and number of adult turtles frequenting the nearby foraging habitats, but it is worth further investigation.

The observed nesting distribution could also be linked to differences in sea surface temperature along the coasts of the sub-basins (Pastor et al., 2020), where the Tyrrhenian is the warmest sea with the highest nest densities. Further research into the correlation of sea surface temperature, warming trends, and turtle nesting activity is needed and out of scope of this review. It also needs to be considered that sea temperature does not influence the distribution of nests directly, but rather plays an important role in the environmental conditions of suitable foraging areas that shape the distribution of adult turtles (Almpanidou et al., 2021).

While many of the nests are still scattered largely over the region, four beaches, Chott Zouaraa in Tunisa and three beaches in the Cilento Park, had regular nesting activity over the past five years. Moreover, two of the Cilento beaches have even reached one of the arbitrary thresholds (3 nests km^{-1} yr^{-1}) which were used by Casale et al. (2018) to distinguish major nesting sites in the Mediterranean. This clearly indicates that nesting on some beaches has become regular and predictable for future nesting seasons. Overall, nest numbers presented here are likely underestimated, since only very few beaches have been monitored intensively and most of the nest detections rely on recognition and reporting of tracks by citizens and beach operators. It might be argued that increased public awareness and advanced communication technologies would lead to an increase in the number of reported tracks or turtles, thus explaining an increase in the overall registered nesting activities. However, tourists and smartphones were already present 10 years ago on most of the beaches where nests are more abundant now, so the increased reporting rate alone cannot account for the steep increase of nest numbers especially during the 2020 season. This finding is also corroborated by the only monitoring that was carried out repeatedly during the study period, specifically on the Cilento beaches, which initially revealed no nests in 2010 but led to the discovery of nests in 2017 and 2020. The authors are thus confident that the increasing number of turtle nests is nonetheless reflecting a real trend and that more turtles are now exploring new nest sites all over the Western Mediterranean.

On the other hand, some nests may never have been discovered because they were made on less touristic beaches or the tracks were extinguished by beach levelling activities, which could as well have destroyed entire clutches. Unfortunately, beach levelling with tractors and bulldozers is quite commonly practiced during the high season in the study area. Instead, nests laid early during the season may also remain undetected since the beaches are less frequented by the public. Finally, many reported nesting attempts were not matched by a successful nest on successive nights on the same or nearby beaches, thus the location where the turtle finally laid its clutch remained unknown, further contributing to the number of undiscovered nests.

We have considered the possibility that females are recruits from some previously unnoticed nesting and found it unlikely, since only a generation ago, beach temperatures were below the pivotal temperature (between 28.5 and 29.3 °C reviewed by Witt et al. (2010) and would not have produced sufficient numbers of females to return to these beaches (Maffucci et al. (2016), see also Carreras et al. (2018)). Based on so little information, the reproductive phenology (e.g., inter-nesting and remigration intervals) of western nesters still warrants further studies. However, novel genetic tools are currently being applied to identify the mothers and fathers of the clutches laid in the expansion area and promising first results have already identified nests belonging to the same female (e.g., nests ES_08, ES_23 and ES_26, Table S1, Carreras et al. (2018)). For the time being, we can largely ascertain a good correspondence between nesting season duration in the Western Mediterranean and eastern rookeries, as well as average clutch size, incubation duration, and hatchling sizes (compared to data reviewed by Casale et al. (2018)). Interestingly, we found that clutch size slightly decreases over the season, which was explained by (Broderick et al., 2003) as resource depletion causing loggerheads to lay smaller clutches late in the season. Further data are needed to confirm this relationship and could provide important information on the reproductive output of Western Mediterranean beaches.

Unfortunately, these exploring females must select their nest sites in beaches which are highly anthropized and hence present them with a lot of challenges. Almost a third of the clutches were relocated because the females laid them too close to the water or in otherwise unsuitable places (e.g., sand mixed with soil and pebbles). Obstacles on the beach can make females nest closer to the waterfront (Witherington et al., 2011), which may be just one explanation for the observed behaviour, since turtles often encountered sunbeds, umbrellas, and gangways during ascent. Females nesting too close to the water may also just prefer to nest in the dark and thus avoid the back of the beaches which are often illuminated by resort/restaurant spotlights on the beach or streetlights (Salmon et al., 1995). Nest relocation, despite the risk of motion-induced mortality of the developing embryos, is commonly applied to save nests that are at higher risk by one or multiple threats (Grand and Beissinger, 1997). The practice has contributed here and elsewhere (Kornaraki et al., 2006; Candan, 2017) to successful incubation and hatchling production, rather than losing some nests entirely.

Notwithstanding the problems of human origin, due to climate warming, Western Mediterranean beaches have already become thermally suitable habitats for sea turtle nesting, as was predicted by Pike (2013a) and initially shown by Maffucci et al. (2016). Overall, hatchling emergence success of Western Mediterranean nests is fairly good and within the lower ranges reported for Eastern Mediterranean rookeries (reviewed by Casale [et al., 2018]). Hatching success was on average slightly lower than HS of the larger loggerhead rookeries in Greece, Cyprus, and Turkey (Broderick and Godley, 1996; Kaska et al., 1998; Margaritoulis, 2005), but it was also variable across our region with comparatively high HS in Italy. Although these data are biased towards the large sample size from Italy, it can be safe to say, that western Mediterranean beaches have the potential to produce, if adequately managed, sufficient hatchlings to sustain future viability of these newly forming nesting aggregations. Some of the new nest sites' incubation durations are below the pivotal incubation duration of 59.9 d calculated by Godley et al. (2001) thus indicating that at least in some of the emerging nest sites sufficient numbers of females are produced, which are fundamental for a successful colonisation (Carreras et al., 2018). However, we must also look beyond the nesting season and consider the fate of hatchlings that disperse in a sea that is still too cold in the winter which may cause low survivorship in the first year of life (Maffucci et al., 2016). These concerning prospects are brightened by the predictions of Witt et al. (2010) that the 15 °C isotherm (i.e., the sea surface temperature threshold that Maffucci et al. (2016) used to forecast hatchling survival) will continuously shift to surround only the Ligurian Sea. The western basin will thus become increasingly favourable to occupation by sea turtles during winter months, which is further corroborated by Cardona & Hays' study (2018) concluding that juvenile turtles encounter almost everywhere in the Mediterranean favourable conditions for development just by drifting with the ocean currents.

Thus, while climate warming turns hitherto unfavourable sea regions into thermally suitable habitats, we may already be witnessing the first case of a loggerhead turtle nesting range expansion from the Eastern Mediterranean, and possibly even from the Atlantic, into the Western Mediterranean. However, most of the here discovered emerging nesting habitats overlap with high levels of anthropogenic disturbance, and the turtles may just end up in an ecological trap that reduces fitness, as foreseen by Pike (2013b), rather than enhancing the population's reproductive output. Pressure on coastal habitats through human development is a worldwide problem, but in the Mediterranean, more than 150 million people live along the coasts of the basin which is also by far the largest global tourism destination, attracting almost a third of the world's international tourists every year UNEP/MAP (2012). Certainly, this has impacted sea turtle nesting in the Eastern Mediterranean long before turtles arrived at its western shores. Nevertheless, the long-term conservation projects on some major rookeries in the Eastern Mediterranean have helped some sea turtle nesting populations to recover and accustomed tourists and stakeholders to the presence and needs of sea turtles during the nesting season (e.g., Katselidis et al., 2013). This has not happened in the Western Mediterranean where turtles now literally encounter humans on the beach, both totally unprepared. Emerging females are often scared off or may not be able to find a place to lay their eggs (see suppl. Fig. S1), which may lead to low nesting success rates as observed here in Spain or by Geringny et al. (2016) in France.

In conclusion, the excitement of seeing turtles nest in new areas is overshadowed by exactly the scenario Pike (2013b) depicted, that the likelihood of successful range expansion is reduced right from the start by the overlapping threat of human development and unawareness. With the results of this study at hand, including the knowledge on the most likely hotspots for future turtle nesting in the Western Mediterranean and on the threats present on these beaches, we call for vigilance of these new precarious habitats and for immediate and continued conservation actions. Such efforts, even at sites with low nesting numbers, may contribute to long-term population increases of the Mediterranean RMU, which is already showing an upward trend (Mazaris et al., 2017). Without the protective measures already set in place, the emerging hatchling from 50 % of the nests would have been lost through disorientation caused by artificial lights (Salmon, 2003). Meanwhile, nest placement parameters (such as beach inclination and elevation above sea) should be assessed in the new nesting beaches, which can provide crucial information on nest site selection and foster evidence-based management of the nesting beaches (Katselidis et al., 2013). There may still be a long way to go before the new nesting boundaries are established in the Western Mediterranean, but fortunately the wealth of experience from other beach conservation projects gives us a head-start.

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.

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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.e02194.

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