Influence of the aquatic environment on the nesting ecology of the Loggerhead Sea Turtle (*Caretta caretta*) in the Mediterranean Sea

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by

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Abstract

Loggerhead turtle populations in the Mediterranean have been depleted due to over fishing and to the degradation of their nesting habitats, their protection requires a better understanding of the utilization of the different ecosystems that they exploit. So far, most studies on sea turtle biology have been carried out on the terrestrial part of their nesting areas, even though they spend modes of their lives in the ocean. How this aquatic environment affects sea turtle behaviour has not been evidently understood yet. The main objective of this study is to investigate how the aquatic environment of loggerhead turtles' nesting and foraging areas in the Mediterranean influences their nesting ecology. Two main approaches were taken, 1) the aquatic environment in which loggerhead turtle nesting areas can be found was modelled using MAXENT (a presence only modelling approach); separately, Multiple Linear regression was used to establish the relationship between Sea Surface Temperature (SST) in foraging areas and the reproductive effort and phenology of turtles nesting in Zakynthos, Greece. Results of the Maxent model suggest that the following aquatic environment enhances the suitability of an area to hold nesting colonies of loggerhead turtles in the Mediterranean: a) warmer sea surface temperatures (SST) at the start (month of May) and at the end (month of September) of the nesting season, b) lower concentrations of *chlorophyll a* at the start and end of the nesting seasons (may and September respectively), and c) steeper ocean floors (represented by the distance to the 50m and 500m isobaths in this study. It is suggested that SST could be related with higher metabolic rates that allow turtles to take advantage of the warmest months of the summer for incubation of eggs, while chlorophyll and bathymetry could be related with a strategy of predator avoidance. On the other hand, data for Zakynthos nesting population was correlated with SST from the Adriatic Sea and the Gulf of Gabès, the two major foraging grounds for this population. In general, warmer waters in the year prior to the nesting season is positively correlated to the number of nests and to an earlier start and end of the nesting seasons, while relationships with more than a year lagged SST are negatively correlated. Understanding how environmental conditions affect population dynamics could be an aid in enhancing biodiversity conservation measures.

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1. Introduction

1.1. Research background

This research thesis addresses how the aquatic environment relates to the nesting ecology of loggerhead sea turtles in the Mediterranean. The following section provides information to understand why this study has been carried out.

1.1.1. *Caretta caretta* in the Mediterranean

Caretta caretta (Loggerhead sea turtle) is one of the two species of sea turtles that nest in the Mediterranean basin, and the one that present the largest population. There is an estimate of 2280-2787 nesting females per year, which is much higher than the 339--360 nesting females of *Chelonia mydas* (Broderick *et al.*, 2002), the other species of sea turtles nesting in the region.

Nesting sites of *C caretta* in the Mediterranean Basin are restricted to the eastern region. The major nesting places are along the coasts of Greece, Turkey, Cyprus and Libya, with Zakynthos Island (in Greece) holding the highest number of nests (Margaritoulis *et al.*, 2003). Other nesting sites have been reported in Israel, Italy, and other countries from the northern coast of Africa such as Egypt and Tunisia.

Mediterranean loggerhead populations have not been an exception to the global trend of extensive research on sea turtle biology during the last 20 years (Hays, 2008). The fact that sea turtles nest on land opens the opportunity to study them during these processes. Much of the information gathered on these animals comes from long term monitoring projects on nesting beaches.

The information gathered by these projects on land coupled with studies in laboratories, has produced important knowledge on the characteristics of their life cycle, which is dominated by aquatic stages. Female loggerhead turtles bury their eggs on a beach, and after 60 days of incubation, hatchlings come out and head to the sea. After reaching the water, they swim in a state of frenzy until reaching deeper waters (Lutz *et al.*, 2003).

When the turtles get to the deeper waters, they spend a few years in an oceanic stage. Upon reaching a certain body size, they establish in neritic foraging areas, where they stay until becoming sexually mature, approximately at 20 years of age. After breeding for the first time, female loggerheads return every 2-3 years to the same beach were they were born to lay eggs; males, on the other hand, never go back on land (Miller, 1997).

Although, many aspects on sea turtle biology have been studied, there are still many questions that need to be answered. As for most populations of marine vertebrates, knowledge on how the aquatic habitat influences their biology is still very limited, due to the difficulties of studies in this type of environment. In fact, much of what is known about their behavioural and physiological responses is from the already mentioned studies on land or in tanks in laboratories. This could substantially differ from what occurs when they are on their natural aquatic environment.

In more recent years, new technologies have allowed scientist to start filling the gap of knowledge on how the aquatic environments influence sea turtle biology. On the one hand, improved Remote Sensing technology, i.e. new sensors and algorithms to retrieve bio-physical parameters of oceanic waters, has made data on this ecosystem to be of better quality and more readily available to scientists. On the other hand, accurate GPS and satellite tracking technologies have made following this animals in the ocean much easier (Polovina *et al.*, 2001; Godley *et al.*, 2008).

1.1.2. Selection of nesting areas by Sea Turtles

Coastal ecosystems encompass littoral terrestrial and aquatic environments, which have strong and direct exchange; they are related through biotic and abiotic processes. The exchange of energy and material between sea and land not only defines the substrate but also the life on it, which gives a dynamic character to the ecosystem (Antworth *et al.*, 2006).

Because sea turtles nest on land, their biology is influenced by these 2 coastal ecosystems (beach and coastal waters) during the breeding season. Which and how the environmental parameters from these ecosystems influence their nesting behaviour are not well understood yet.

One of the aspects of nesting behaviour that has called the attention of scientists is nest-site selection. This behaviour is a maternal effect that contributes to offspring survival and variation of phenotypes, which in turn are subject to natural selection (Antworth *et al.*, 2006). For this reason, the understanding of this process would be a great advance in the formulation of policies towards the conservation of sea turtles.

Until now, most studies on selection of nesting sites by turtles have focused on factors that determine choosing a particular spot for nesting on the beach. Factors such as soil grain size, vegetation cover, distance to vegetation, distance to high tide line, humidity and temperature of the sand have been shown to influence this behaviour (Kamel & Mrosovsky, 2004; Karavas *et al.*, 2005; Mazaris *et al.*, 2006; Pike, 2008a).

Most of these studies have only characterized the terrestrial parameters in the nesting beaches, but the scientific community has failed to determine what factors makes turtles choose one beach over another, both with apparently similar characteristics as nesting sites. Furthermore, most of these studies on characterizing nesting environments have focused their attention on local terrestrial parameters, forgetting about the aquatic environment.

The oceanic environment has been proven to play a fundamental role in the biology of sea turtles (Hays, 2008), and most probably the coastal aquatic environment might do so as well, especially having an effect on the selection of a particular beach by sea turtles as a nesting site. Sea Surface Temperature (SST), *chlorophyll a* (Chl a.), ocean currents, bathymetry, geomagnetism, wind stress, solar radiation are some of the aquatic environment parameters that have been proven to have some effect in the oceanic life stage of sea turtles.

A recent study by Moin (2007) was the first attempt to model loggerhead turtle nesting environments in the Mediterranean using variables from the aquatic environment. Although this study is a good starting point, it can be improved in order to reach more solid conclusions, as stated by the author in his recommendations section.

Moin reached the conclusion that SST is an important variable in determining the suitability of an area to be a sea turtle nesting site, nonetheless, it should be remarked that only data for 2 years (May and September data) was used to develop the model. Two years of data might result not representative of the general conditions of the Mediterranean for this SST and could have yielded spurious results, therefore a wider time span should be used.

Furthermore, temperature data were not equally important between years (Moin pers comm.). For example, SST in May of 1996 is an important variable in his model, but on the contrary, SST in May of 1995 was not. A similar thing occurs with SST from July and September. This gives space to raise the question if the mean SST in the nesting areas is important or not for the nesting of sea turtles.

If these inconsistencies are addressed, and other aquatic variables that have been shown to influence sea turtles (e.g. *chlorophyll a*, sea surface height, etc) are included, an improved model of aquatic environmental conditions that make certain places suitable for sea turtle nesting could be done.

Moreover, in the Mediterranean there are 4 genetically distinct nesting populations in the region (Encalada *et al.*, 1998; Carreras *et al.*, 2007; Casale *et al.*, 2008b). The two largest genetically distinct populations are those nesting in Greece (Greece and North Africa) and Turkey. Even though they share feeding grounds to a certain extent, when migrating to the nesting areas they still go to their specific nesting site each year, even if there are seemingly suitable nesting areas on the way.

Distinction on which environmental variables are important to a specific population (if they are different) could be an important contribution in the understanding of their ecology. Potential measures for conservation can be taken by considering the environmental requirements for each of the populations.

1.1.3. Loggerhead turtles in foraging grounds

The Adriatic Sea and the Gulf of Gabès (Tunisia) have been identified as the major foraging grounds for turtles nesting in Greece, accounting for 42% and 28% respectively of post-nesting destinations for this rookery (Margaritoulis & Demetropoulos, 2003; Lazar *et al.*, 2004; Maffucci *et al.*, 2006; Zbinden *et al.*, 2008). Furthermore, the Gulf of Gabès along with other points along the coast of North Africa has been identified as foraging grounds for loggerheads and green turtles nesting in Cyprus (Godley *et al.*, 2003; Broderick *et al.*, 2007).

Determining which are the foraging areas for sea turtles has given the opportunity to understand (or research on) many processes of their life cycle (Encalada *et al.*, 1998; Maffucci *et al.*, 2006; Hochscheid *et al.*, 2007; Casale *et al.*, 2008a), such as their breeding effort and phenology. Loggerhead turtles are mostly non annual breeders that present large fluctuations in nesting numbers. Breeding may be dependent upon reaching a threshold body condition that might be influenced by feeding conditions (Broderick *et al.*, 2001). These, in turn, can be influenced by environmental conditions.

Variation in environmental conditions may determine whether or not an individual breeds at all in a given year. This leads to variation in the numbers of individuals breeding each year, and are likely to be factors driving variations in remigration intervals (years between successive nesting for a female sea turtle).

Female turtles generally require at least 8 to 10 months for acquiring sufficient body fat deposit for vitellogenesis (egg formation) to occur in the foraging grounds (Hamman *et al.*, 2003), and even more to fulfil the energy requirements needed for migration and nesting .

Sea surface temperature, *chlorophyll a* concentration and net primary productivity are three of these conditions that are expected or have been shown to affect in one way or another breeding of sea turtles. Chaloupka *et al* (2008) found that there is an inverse correlation between nesting abundance and mean annual SST in the core foraging regions for 2 loggerhead populations (Japan and Australia) during the year prior to the summer nesting season.

In other study, Saba *et al* (2007) found that the El Niño Southern Oscillation has an effect on the reproductive frequency of eastern Pacific leatherback turtles because of warm, less productive oceans. Moreover, Saba *et al* (2008) showed that ENSO has an effect on Net Primary Productivity that significantly influences the nesting ecology of leatherbacks at the Pacific Coast of Costa Rica. *Chlorophyll a* is related to phytoplankton concentration in an area, which gives an insight of the primary productivity in a specific region of the ocean.

Also, SST has been shown to be a factor affecting marine turtle nesting activity Water temperature in breeding areas during the nesting season has an effect on the nesting phenology (Hays *et al.*, 2002; Solow *et al.*, 2002; Mazaris *et al.*, 2004). Phenology, defined as the timing of seasonal activities.

Furthermore, Broderick et al. (2001) studied the inter-annual variation of nesting numbers in populations of green and loggerhead turtles in the Mediterranean, finding that it was different between species, with greens having a longer remigration period. She suggests that these differences are due to varying trophic statuses of the different species; green turtles are herbivores, thus their feeding is more dependent on primary production, which in turn will be more tightly coupled with the prevailing environmental conditions than the carnivorous diet of the loggerheads.

Fidelity to nesting grounds has been widely proven for sea turtles, and recently it was found that sea turtles nesting in Cyprus present a high fidelity to migration routes and foraging grounds (Broderick *et al.*, 2007). They were able to place satellite transmitters to the same turtles (6 in total) over consecutive breeding seasons, and saw that the turtles were using very similar migrating routes and foraging grounds.

In the last glacial era 15000 years ago , loggerhead populations went extinct in the Mediterranean Sea due to their inability of moving to warmer waters (though re-colonized 12000 years ago by individuals from the Atlantic population) (Bowen, 2003). Climate change is a great concern nowadays, in case of an increase or decrease of sea surface temperature, these populations could face extinction again.

1.2. Problem Statement

There is evidence that loggerhead sea turtle stocks in the Mediterranean have been depleted. Fishing pressure, human exploitation, and restriction and degradation of their nesting areas have been identified as the main causes (Margaritoulis & Demetropoulos, 2003; Canbolat, 2004; Casale *et al.*, 2004; Lazar *et al.*, 2004). *C. caretta* is considered as threatened in the region under various international and national listings; for example, , it is facing a very high risk of extinction in the wild in the near future according to the ‘‘Red List of Threatened Species’’(IUCN, 2007).

The protection of loggerhead turtles and their habitats (by means of land use planning, fisheries management, coastal conservation and other measures) should be enhanced. In order to formulate effective conservation policies, a better understanding of the utilization of the different ecosystems that they exploit in the different stages of their life cycle is required (Antworth *et al.*, 2006).

So far, most studies on sea turtle biology have been carried out in their nesting areas, especially on land. These studies have allowed scientists to estimate that sea turtles spend no more than 1% of their life cycle on land, and spend the rest in the ocean. In spite of this fact, influences of the aquatic environment on sea turtle behaviour are not yet well understood are the subject of many hypotheses (eg. Chaloupka *et al.*, 2008). Understanding how the conditions in their aquatic environment affect the nesting ecology of sea turtles could lead to more efficient monitoring and management of the different species.

Moreover, global climate change is considered to be one of the major threats that biodiversity is facing. Therefore exploring the effect of climatic variability on the aquatic environment of sea turtles (e.g. breeding and feeding areas) could be essential in the protection of this species (Chaloupka *et al.*, 2008; Mazaris *et al.*, 2008).

1.3. Research objectives

1.3.1. General Objective

The main objective of this study is to investigate how the aquatic environment of loggerhead turtles’ nesting and foraging areas in the Mediterranean influences their nesting ecology.

1.3.2. Specific objectives

1. To characterize Sea Surface Temperature, *Chlorophyll a* concentration, Sea Surface Height, Wind Stress and Bathymetry in the coastal waters near known nesting beaches of loggerhead turtles in the Mediterranean basin.
2. To improve a regional model of suitable coastal aquatic environments for loggerhead turtle nesting in the Mediterranean basin using the parameters from objective one.
3. To relate temporal annual variability of Sea Surface Temperature in the foraging grounds (Adriatic Sea) of loggerhead turtles nesting in Greece to their nesting effort and phenology.

1.4. Research questions

1) Is there a significant difference between the values of the aquatic parameters in sites where nesting has been reported and places where it has not been reported, and if there is, which are this values?
2) Can SST be confirmed as an important parameter for modelling the suitability of a coastal area for sea turtle nesting in the Mediterranean basin?
3) How does including chlorophyll a, sea surface height and wind stress can enhance the modelling of suitability of aquatic coastal areas for sea turtle nesting in the Mediterranean?
4) Are the most important aquatic environment parameters that determine the suitability of a coastal area for loggerhead turtle nesting in the Mediterranean different between the population nesting in Greece and the one nesting in Turkey?
5) How is the annual variability of Sea Surface Temperature in the Adriatic Sea related to the nesting effort and phenology of loggerhead sea turtles? Characteristics to be assessed:
    a. Total number of nests
    b. Average clutch size (average number of eggs per nest)
    c. Total duration of nesting season
    d. Start and end dates of nesting season.

1.5. Hypothesis

Ho_1: There is not a significant difference in the values of aquatic environment parameters between areas in the Mediterranean, so that no distinction between areas suitable for sea turtle nesting can be made.
Ha_1: There is a significant difference in the values of aquatic environment parameters between areas in the Mediterranean, which make some of these more suitable for the nesting of sea turtles.

Ho_2: SST is not an important aquatic environmental parameter for modelling the suitability of a coastal area as a loggerhead turtle nesting site in the Mediterranean.
Ha_2: Given an appropriate time span of SST data can confirm that SST is an important variable that determine the suitability of an area to hold loggerhead nesting populations.

Ho_3: Including *chlorophyll a*, sea surface height and wind stress will not enhance a model of suitability of aquatic coastal environment for sea turtle nesting in the Mediterranean that uses only SST, radiation and bathymetry.
Ha_3: Including *chlorophyll a*, sea surface height and wind stress can enhance the modelling of suitability of aquatic coastal environment for sea turtle nesting in the Mediterranean.

Ho_4: Important aquatic environment parameters that determine the suitability of a coastal area for loggerhead turtle nesting in the Mediterranean are the same for the two genetically distinct populations that nest in Greece and Turkey?
Ha_4: Importance of SST, *Chlorophyll a* and topography of the ocean floor between the coasts of Greece and the coasts of Turkey will be distinct.

Ho_5: The temporal variability of Sea Surface Temperature in the Adriatic Sea is not related to the total number of nests in Zakynthos.
Ha_5: Higher temperature in foraging areas during the year prior to nesting is positively correlated with number of nests in breeding areas, and with the length, start and end of the nesting seasons.

2. Methodology

In this section, the study area, environmental variables, data preparation and data analysis are described. For a summary of the methodological approach, see Figure 2 in page 17.

2.1. Study area

The study area in which the first 2 objectives are focused is the Mediterranean Basin as a whole (Fig.1). For the third objective, the sea surface temperature for 2 specific places is determined; the Adriatic Sea and the Gulf of Gabès (the 2 main foraging areas for loggerhead turtles nesting in Zakynthos). These three areas are shortly described in this subsection.

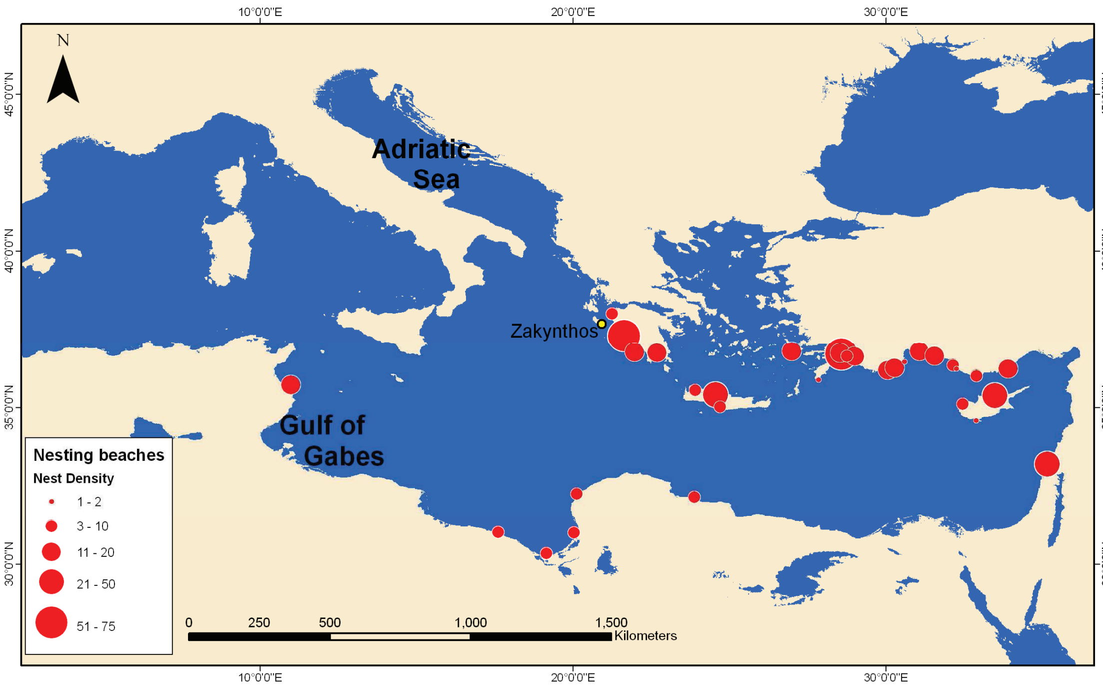

Figure 1. Map of the Mediterranean Basin, with the location of the Adriatic Sea and the Gulf of Gabès indicated. Red points on the map represent known loggerhead turtle nesting sites; Zakynthos Island (which holds the largest population of loggerhead nesting in the Mediterranean) is represented by a yellow point.

2.1.1. Mediterranean Sea

The Mediterranean Sea is a semi-enclosed basin, situated between Europe, North Africa and West Asia. It covers an area of about 2,512,000 km^2. It has an east-to-west length of about 3860 km and a maximum width of about 1600 km (Margaritoulis *et al.*, 2003). Generally shallow, with an average depth of 1500 m, it reaches a maximum depth of 5150 m off the southern coast of Greece.

This sea is connected to the Atlantic Ocean by the Strait of Gibraltar. It is divided into two main basins, which are separated by the shallow Strait of Sicily (Marullo *et al.*, 1999). The Western basin includes the Alboran, Catalan, Balearic, Ligurian and Tyrrhenian sub-basins, while the Ionian, Adriatic, Aegean and Levantine sub-basins make up the Eastern Basin.

A great range of processes and interactions occurs within the Mediterranean, which is characterized by a thermohaline circulation. The scarce inflow of water, coupled with high evaporation, makes the Mediterranean much saltier than the Atlantic Ocean. Evaporation is especially high in its eastern half, causing water level to decrease and salinity to increase eastward (Garcia-Gorriz & Vazquez-Cuervo, 1999).

2.1.2. Adriatic Sea

The Adriatic Sea is the northernmost basin of the Mediterranean Sea, lying between the Italian and Balkan Peninsulas. It extends northwest from 40° to 45° 45'N, connecting with the Ionian Sea (Janekovic *et al.*, 2006) to the south. It is about 800 km long with an average width of 160km, and an area of 131050 km^2.

Three regions can be identified. The Northernmost region extending to the latitude of Ancona, in Italy, is shallow with depths of no more than 100 meters. To the South of this, the topography drops quickly to more than 200m in the Jabuka Pit, which is separated from the third and deepest part of the Adriatic by the Palagruza Sill. This southern part reaches a depth of 1324m, and rises up again to a 780m depth in the Strait of Otranto where it meets the rest of the Mediterranean (Poulain, 1999).

The mean surface circulation in the Adriatic Sea consists of a basin-wide cyclonic gyre. Water enters on the east from the Ioninan in the east and floes northward along the Balkan coast. Along the Italian side, water flows south, re-entering the Ionian Sea on the west part of the Otranto strait (Notarstefano *et al.*, 2006). Oceanographic conditions are subject to great seasonal and inter-annual variations (Gacic *et al.*, 1997).

2.1.3. Gulf of Gabès

The Gulf of Gabès is situated in the south Ionian Sea, occupying a wide continental shelf area along the east coast of Tunisia (Bel Hassen *et al.*, 2009). It is nearly 100 Km long and 100 km wide, bounded by the Kerkena Islands on the northeast and by Djerba islands in the southeast.

Except for the Strait of Gibraltar and the Gulf of Venice, it is the only part of the Mediterranean with a substantial tidal range (about 2.5 m at spring tides), causing the uncovering of extensive sandbanks at low water. Sponge and tuna fisheries are located at the main ports of Gabès and Sfax.

2.2. Data

2.2.1. Species Data

Species data for the present study was obtained from literature. Following, a short description on the type of data and the sources is given.

2.2.1.1. Nesting sites in the Mediterranean

Data on Loggerhead nesting localities used in this study was obtained from a database compiled by Moin (2007). An extensive literature review was carried out in an attempt to extend this database; nonetheless all the relevant reported nesting sites for *C. caretta* were already incorporated.

The database (Appendix A) is comprised of 34 nesting sites, for which longitude, latitude, extent of the beach, average number of nests per year and nest density is reported. This data base was generated based on information obtained from peer-reviewed publications; for more information on sources see Moin (2007).

2.2.1.2. Nesting activity in Zakynthos Island, Greece

The major nesting location reported in the Mediterranean Basin is Laganas Bay, located on the island of Zakynthos, Greece. A long term monitoring project with standardized methods for data collection has been carried out since the early 1980’s by the NGO Archelon.

For this study, the following annual nesting data was obtained for this place:

- Number of nests.
- Average clutch size (the total number of eggs laid per female per nest).
- Date of first emergence of a female to the beach (start of the nesting season).
- Date of last emergence of a female to the beach (end of nesting season).

Data for the period 1984-2002 was obtained from Margaritoulis (2005). Data for the number of nests from the year 2003 until 2008 was obtained from the Archelon website (Archelon, 2008; www.archelon.gr).

2.3. Environmental Data

From a list of candidate predictor variables that were considered at some point to include in the modelling of suitable aquatic environment for nesting of loggerhead turtles, 5 of them were finally selected based on a literature revision. These variables are: Sea Surface Temperature, *Chlorophyll a* concentration, Sea Surface height deviation, Wind Stress, and Bathymetry

The variables were chosen on the basis of literature review. A short review of why these variables were chosen follows below, and a short description on the obtained data is provided in Table 1.

1. **Sea Surface Temperature (SST)**

   SST has been found to be used as an orientation cue by sea turtles (McMahon & Hays, 2006); it has been correlated with the length of the nesting season and the inter-nesting period (Chaloupka & Limpus, 2001; Hays *et al.*, 2002; Hawkes *et al.*, 2007; Saba *et al.*, 2007; Chaloupka *et al.*, 2008; Eckert *et al.*, 2008; Mazaris *et al.*, 2008; Pike, 2008b). Furthermore, SST affects the metabolism of animals, and warmer temperatures could indicate higher metabolic rates.

2. *Chlorophyll a* concentration (Chl a)

Chlorophyll a is used as an indicative of primary productivity levels, thus of forage availability. Sea turtles could nest in waters where prey availability is high, but on the other hand, this type of places could imply that the presence of potential predators for the hatchlings would increase as well. Moreover, the attenuation of light underwater increases exponentially with surface *chlorophyll a*, thus, clear waters could result beneficial to active predators such as sea turtles (but also for potential predators of hatchlings).

3. Sea Surface height deviation (SSHa)

SSHa deviation is the difference between the measured and the expected mean SSHa. The topography of the ocean is important for understanding the fundamental processes behind ocean currents. Oceanic pressure centres can drive ocean currents much like atmospheric pressure centres drive atmospheric winds (Ducet *et al.*, 2000). SSHa deviation is used in this study instead of geostrophic currents, due to the fact that no accessible data set for the Mediterranean basin was available in monthly resolution; it has also been used in another study linking it with sea turtle behaviours (Eckert *et al.*, 2008; Kobayashi *et al.*, 2008), allowing for comparison.

Several studies have linked surface currents with adult sea turtle movements (Morreale *et al.*, 1996; Luschi *et al.*, 2003), and with hatchling and juveniles distribution in the ocean (Lohmann, 1991; Goff *et al.*, 1998). During their oceanic movements adult sea turtles swim both with and against prevailing currents (Seminoff *et al.*, 2008), thus it might be possible that this variable does not affect them much while remaining on coastal areas during nesting season.

4. Wind Stress (WS)

Strong wind-driven circulation in the section of the water column can occur, giving place to upwelling events (e.g., Smith, 1968) that can affect productivity and sea turtle movements. They have also been hypothesized to have an effect on the carapace of adults when submerging to breath. Moreover, strong winds on the sea surface might have an effect on hatchlings when reaching the water.

5. Bathymetry

Bathymetry has been linked to sea turtle movements (Morreale *et al.*, 1996; Hays *et al.*, 2001; Luschi *et al.*, 2003). Furthermore, hatchlings need to get quickly to deeper water in order to reduce the risk of predation; therefore places with steep coastal topography could be beneficial for them. For this study, the distance to isobaths every 50 meters from the coastline, up until the 600m isobaths was determined.

Table 1. Overview of remote sensing data products used in the present study. Except for bathymetry data, all the data was obtained from NOAA's Ocean Watch Catalogue (http://oceanwatch.pfeg.noaa.gov: 8081/thredds)

Variable	Spatial resolution	Accuracy	Temporal resolution	Source
SST- AVHRR Pathfinder v5 day & night	0,05 X 0,05 degrees	± 0,3 °C	1985-2007	NODC[a] and the RSMAS[b]
MODIS chlorophyll a concentration	0,05 X 0,05 degrees	40%	2002-2008	NASA Goddard's Space Flight centre
AVISO SSHa deviation	0,25 X 0,25 degrees	unknown	1992-2008	Centre National d'études Spatiale
Wind Stress	0,25 X 0,25 degrees	± 0.01 Pa	1992-2008	Quick SCAT
Bathymetry- ETOPO 1	1 arc-minute	± 1 arc-minute	-	National Geophysical Data Centre (NOAA)

[a.] National Oceanographic Data Centre
[b.] Rosentiel School of Marine and Atmospheric Sciences

2.4. Data preparation

Data sets were processed in order to extract the values of each variable in the nesting areas and at randomly selected points. The images were aggregated using the ITC Integrated Data Viewer, producing images with the mean values for each month from April until October, months that represent the nesting season of loggerheads in the Mediterranean.

During the month of April, adults reach coastal waters where they mate, from April until early September female turtles nest. From July to October hatchlings emerge from the nests and enter the ocean.

The produced grids were exported from IDV as CSV files and imported into Arc Map. Shape files were firstly produced with the add X and Y tool, and afterwards converted into Raster images. On the other hand, contour lines from the coastline and islands, and from the different isobaths (50m, 100m, 150m, 200m, 250m, 250m, 300m, 350m, 400m, 450m, 500, and 600m) were created using the ETOPO1 raster.

A point file with the location of the nesting beaches was created. As well, 2000 random points were created along the contour line of the Mediterranean coast, in order to represent potential unknown sea turtle nesting sites. The "Near" tool in Arc Map measures the distances from a point to the nearest line. It was used for measuring the distance to the different isobaths.

Following the same approach as Moin (2007), both the presence and the random points were moved 2Km offshore in order to extract SST, *Chlorophyll a* concentration and Sea Surface Height. These points were moved further into the ocean in order to extract the Wind Stress data, at about 20Km from the coast line.

Finally, a smaller subset of the Pathfinder SST data from the Gulf of Gabès and the Adriatic Sea was obtained using IDV. Images were to produce a record of mean sea surface temperature for 1 year. For this study, a year was taken as the 12 months before the start of each nesting season (e.g. from April 1993 to March 1994, from April 1994 to March 1995, etc.).The results were taken into Arc Map were the land pixels were masked, and the mean temperature of the remaining image was extracted.

2.5. Data Analysis

2.5.1. Habitat characterization

After obtaining all the values for the different predictor variables, descriptive statistics were calculated. As well, one way analysis of variance (ANOVA) was performed in order to asses the following:

- Difference in the values of each of the aquatic environmental variables between nesting areas.
- Difference in the values of the aquatic environmental variables between nesting and non-nesting places.

2.5.2. Modelling the aquatic environment in front of loggerhead nesting sites

In order to model the aquatic environment of the coastal areas where loggerhead turtles nests in the Mediterranean Basin, the MAXENT method proposed by Phillips *et al.* (2004;) was used. This model has been widely discussed in recent years; therefore this document will discuss only the characteristics that make it appropriate for this study.

Maxent is a general-purpose algorithm that can generate predictions or inferences from an incomplete set of information, for example a set of presence only data for a specific species (*C. caretta* in our case). This method is based on the assumption that it is possible to approximate a target species probability distribution by finding the probability distribution of maximum entropy (the closest to uniform) subject to a set of constraints (Phillips *et al.*, 2004; Phillips *et al.*, 2006). This set of constraints is the expected value of what we know about the species, in this case the empirical average for a set of environmental variables obtained from presence points. These environmental variables are what we know about the target distribution.

For this study, the input data includes a set of samples (nesting sites) and a background file. The samples file includes the coordinates and values for the environmental variables from each of these locations. The background file includes the same information as the samples file, but instead of the presence data, it contains data for random locations from the same geographical space in which the study is taking place.

Maxent, like most maximum likelihood approaches, performs a number of iterations in which the weights are adjusted to maximize the average probability of the point localities, expressed as training gain. The gain is closely related to deviance, a measure of goodness of fit used in General Additive Models and Generalized Linear Models. It starts at 0 and increases towards an asymptote during the run, indicating how closely the model is concentrated around the presence samples.

To evaluate the model performance, Maxent provides several statistical measures. One of them is the Receiver Operating Characteristic (ROC) Curve (AUC). According to Phillips (2006), the AUC measures how well a classifier distinguishes between sites with positive instances (presence localities) and negative instances (background localities). A random model has an AUC of 0.5, therefore the closer to 1 that the AUC becomes, the better our model is. In the case of using test localities, if the AUC for these and the training data are close, it means that there is no over fitting of the model (Saatchi *et al.*, 2008).

Furthermore, Maxent uses a Jack-knife test to provide variable importance statistics. The output is a plot with a red line representing the gain of the model using all the variables. For each variable, a line (black in this case) representing how much gain the model would have if this variable is taken out, and a line (grey) representing how much gain a model with only this variable has is provided. Comparing these 3 values suggest a result of the importance of each variable.

In this study 120 presence samples were used. These samples were obtained by assigning weights to the 34 points mentioned in section 2.2.1.1 according to nesting density (Appendix B). They were further divided into 5 different partitions of training and test points in order to aid with the evaluation of the model. 70% of the presence points were used for training the model and 30 % for testing.

Other types of partition were done with the presence samples; it was partitioned as to represent only sea turtles from the Greek (Greece and North African population) and only from the Turkish (Turkey and Cyprus) populations.

Finally, before carrying on with the model, a correlation matrix was performed on the environmental variables in order to establish possible co-linearity amongst them. Co-linearity, if present, can made the results difficult to interpret

2.5.3. Relation of SST in foraging areas with nesting effort

A Multiple Linear Regression (MLR) analysis was used as the analytical approach to establish a relation between SST of foraging areas and nesting effort and phenology of sea turtles in Zakynthos Island, Greece. A short explanation on MLR is given in the following paragraphs, and is a review of statistical books by Zar (1996), and Quinn and Keough (2002)

Multiple linear regression attempts to model the relationship between two or more explanatory variables and a response variable by fitting a linear equation to observed data. Every value of the independent variable x is associated with a value of the dependent variable y. The population regression line for p explanatory variables x1, x2,…., xp is defined to be $\mu_y = ß_0 + ß_{1x1} + ß_{2x2} + \dots + ß_{pxp}$.

This line describes how the mean response changes with the explanatory variables. The observed values vary for y about their means μ_y. The fitted values b0,…., bp estimates the parameters $ß_0 + ß_{1\dots}$ $ß_p$ of the population regression line.

Since the observed values for y vary about their means μ_y, the multiple regression models include a term for this variation. This means that the model is expressed as data = fit + residual. The "residual" term represents the deviations of the observed values y from their means μ_y, which should be normally distributed with mean 0.

In the least-squares model, the line of best fit for the observed data is calculated by minimizing the sum of the squares of the vertical deviations from each data point to the line (if a point lies on the fitted line exactly, then its vertical deviation is 0). Because the deviations are first squared, then summed, there are no cancellations between positive and negative values.

This statistical technique was used to create 5 different models. Each model used one of the following nesting characteristic as a response variable: a) number of nests, b) average clutch size (number of eggs per nest in each season, c) total length of the nesting season, d) start date of the nesting season, e) end date of the nesting season.

For each of the models, SST in the Adriatic Sea and the Gulf of Gabès was used as the predictor variable. The approach took into account lagged relations with lagged SST, e.g. if the number of turtles nesting on the year 2005 was related to the SST from one year before the nesting season (in this example April 2004-March 2005), 2 years (April 2003-March 2004) and 3 years before (April 2002-March 2003). From this point onwards this will be referred to as 1, 2, or 3 year-lagged SST.

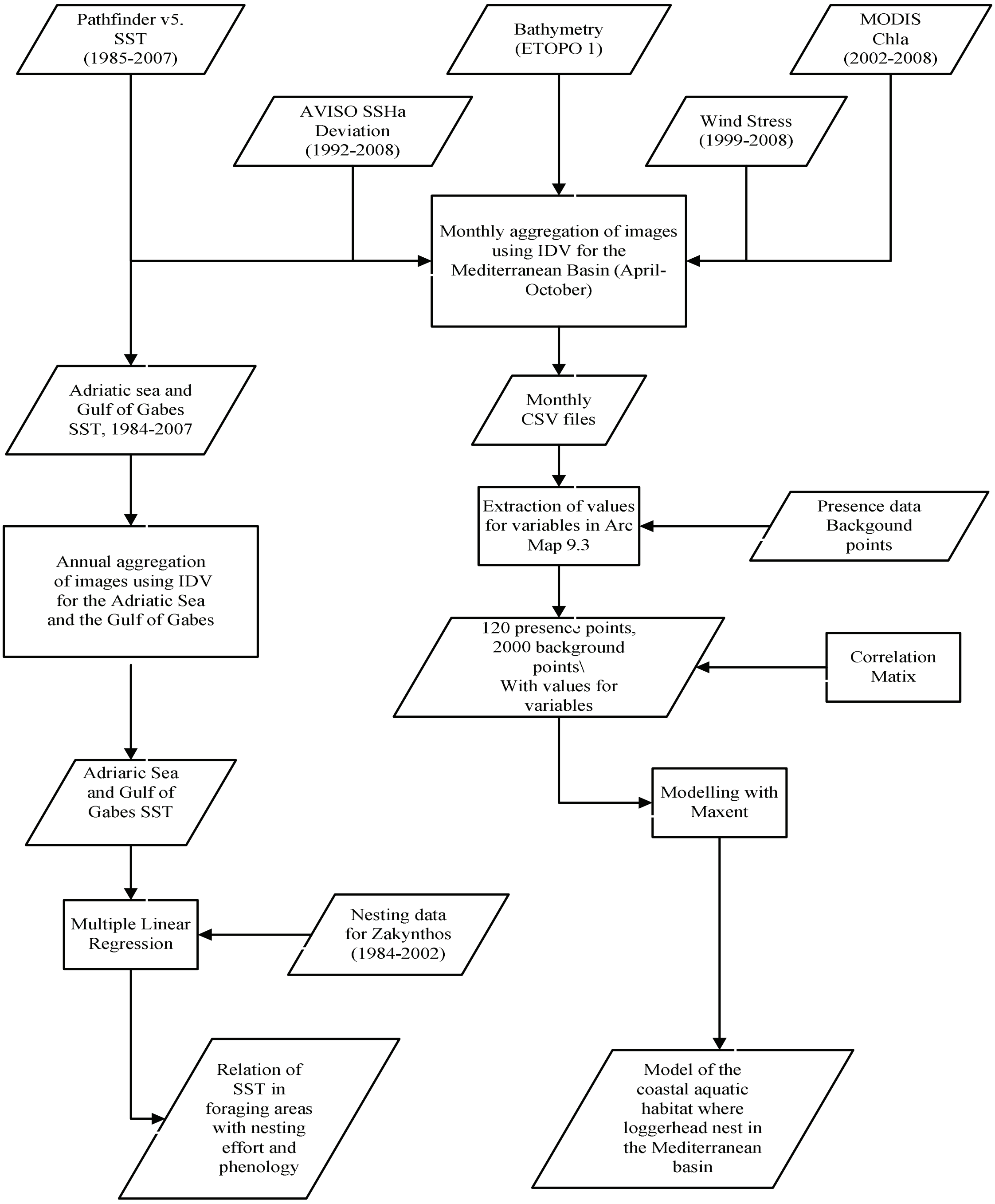

Figure 2. Flowchart summarizing the methodological approach taken in this study.

3. Results

3.1. Habitat characterization

This subsection provides a general characterization of the environmental variables that were proposed as predictor variables for modelling the aquatic environment nesting in areas where loggerhead turtles nest in the Mediterranean Basin. First, each variable for every month was characterized in the nesting area. Second, a comparison of variable values in May and in September will be done (for reasons that will be explained in section 3.2.2) between locations where nesting has been recorded. Third, a comparison for the variables in these 2 months between places where nesting has been recorded and where it has not.

3.1.1. Descriptive statistics

The mean SST obtained from the months of May-October was 23,39 ± 3,66 °C, with the minimum temperature being in April and the maximum in August (Fig 3a). Mean *Chlorophyll a* concentration was 0,325 ± 0,978 mg/m^3, tending to increase from April to September; nonetheless some of the nesting sites present very high values (Fig 3b). Average Wind stress was 0,0513 ± 0,025 Pa (Fig 3c). Mean SSHa deviation (Figure 3d) tend to be negative in the first months of the nesting season and positive in the last months (SSHa deviation is the deviation from the mean, therefore a seasonal mean is not estimated because it is close to 0). Distance to isobaths tendency can be observed in Figure 3e.

3.1.2. Characteristics in May and September

A paired t-test was performed in order to test if the environmental conditions were different at the beginning and at the end of the nesting seasons, represented by the months of May and September. Table 2 shows how that there is no a significant difference between the *chlorophyll a* concentrations, but there is a significant difference between the two months for SST and SSHa

3.1.3. Comparison between places where nesting has been reported and places where it has not been reported.

Mean and standard deviation for the aquatic environmental variables can be observed in table 3. Sea surface temperature is higher in localities where nesting of loggerheads has been reported than in places where it has not been reported for both May ($F= 21,949$, $df= 1044$, $p<0,001$) and September ($F= 19,928$, $df= 1044$, $p<0,001$).

Concentration of *chlorophyll a* is significantly lower for the months of May ($F= 3,291$, $df= 1044$, $p<0,05$) and September ($F= 5,034$, $df= 1044$, $p<0,05$) in localities were nesting is known to occur. A similar pattern can be observed with the distance to the 50 m isobaths ($F= 3,842$, $df= 1044$, $p= 0,05$) and 500 isobaths ($F= 7,116$, $df= 1044$, $p<0,05$), which is shorter from coasts where loggerhead turtle nesting has been reported.

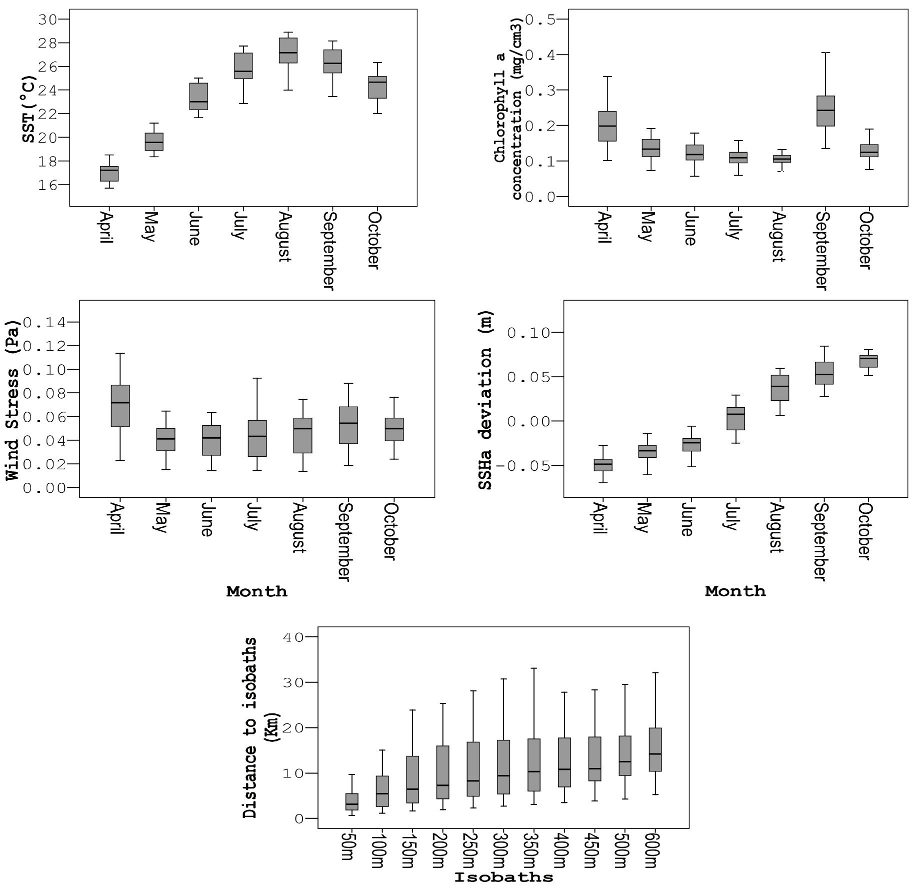

Figure 3. Monthly characteristic values for a) Sea Surface Temperature, b) *Chlorophyll a* concentration, c)Wind Stress, d)Sea Surface Height, and 2) distance to isobaths in locations were nesting of *Caretta caretta* has been reported in the Mediterranean Basin.

Table 2. Results of the paired t-test comparing variables at the beginning (May) and end (September) of the nesting season in sites were loggerhead turtle nesting is known to occur in the Mediterranean.

Paired variables	t	df	Probability
Chlorophylla May - Chlorophyll a September	-.824	33	0.416
SST May - SST September	-79.7	33	<0.001
SSHa May - SSHa September	-37.8	33	<0.001

Table 3. Mean and standard deviation of variables in locations at know nesting sites in the Mediterranean Basin, and at randomly chosen sites from which nesting has not been reported.

Variable	Nesting sites		Non nesting	
	Mean	Std dev	Mean	Std dev
SST May (°C)	19,51	0,79	18,27	1,20
SST September (°C)	26,23	1,11	24,67	1,75
Chlorophyll May (mg/m3)	0,13	0,03	0,51	1,16
Chlorophyll September (mg/m3)	0,24	0,10	0,78	1,92
Distance to 50m isobaths (km)	4,37	5,65	8,99	21,50
Distance to 500m isobaths (km)	17,21	28,02	54,57	95,65

3.2. Modelling the aquatic environment of loggerhead turtle nesting sites

3.2.1. Correlation matrix

After performing the correlation matrix between the variables used in this study, wind stress data was left out of the candidates variables incorporated into the Maxent algorithm. Wind stress and sea surface temperatures from all the months showed to be highly correlated (Table 4), and thereof could not be incorporated as truly independent variables. SST was preferred over WS because of its better spatial resolution and nominal accuracy. Furthermore, this study targets conditions closer to the cost (whenever possible), for which SST is better suited.

As expected, there was a correlation between monthly values for each variable. For this reason, in an attempt to reduce the co linearity effect in the model, it was decided only to use the months of May, July and September as indicators of the start, middle and end of the nesting season. This same approach was taken by Moin (2007) in his study, so continuing with this method also allows for a better comparison. Finally, all depths were strongly correlated with one another. For this reason the distance to the 50m, 250m and 500m isobaths were used for modelling.

Table 4. Correlation Matrix between Sea Surface Temperature (SST) and Wind Stress (WS) for areas of Loggerhead Turtle nesting in the Mediterranean Basin.

		SST April	SST May	SST June	SST July	SST August	SST September	SST October	SST Season
WS May	R	-.503	-.696	-.801	-.787	-.699	-.679	-.561	-.739
	Sig	0,002	0,000	0,000	0,000	0,000	0,000	0,001	0,000
WS July	R	-.532	-.686	-.784	-.849	-.803	-.788	-.682	-.790
	Sig	0,001	0,000	0,000	0,000	0,000	0,000	0,000	0,000
WS September	R	-.404	-.536	-.612	-.631	-.529	-.571	-.499	-.588
	Sig	0,018	0,001	0,000	0,000	0,001	0,000	0,003	0,000

3.2.2. Modelling for the entire Mediterranean basin

The following step was to model (using Maxent) the coastal aquatic environment in sea turtle nesting areas including all the variables, in order to recognize the ones that showed more importance and eliminate non-relevant variables. The resulting variables with the highest importance were used in subsequent runs in order to achieve the best model to predict presence of loggerhead turtles nesting in a particular site.

The result can be observed in the jack-knife plots for the training set gain and the test set gain (Fig 4). The total gain of the models when all the variables are included is represented by the red bar. The first remarkable result is that when SSHa was used alone in the models, none of the moths showed considerable gain (grey bar in the plots). Furthermore, the model does not lose any gain when they are not taken into account (black bar in the plots). For these reasons, all variables pertaining SSHa were removed from subsequent runs of the model.

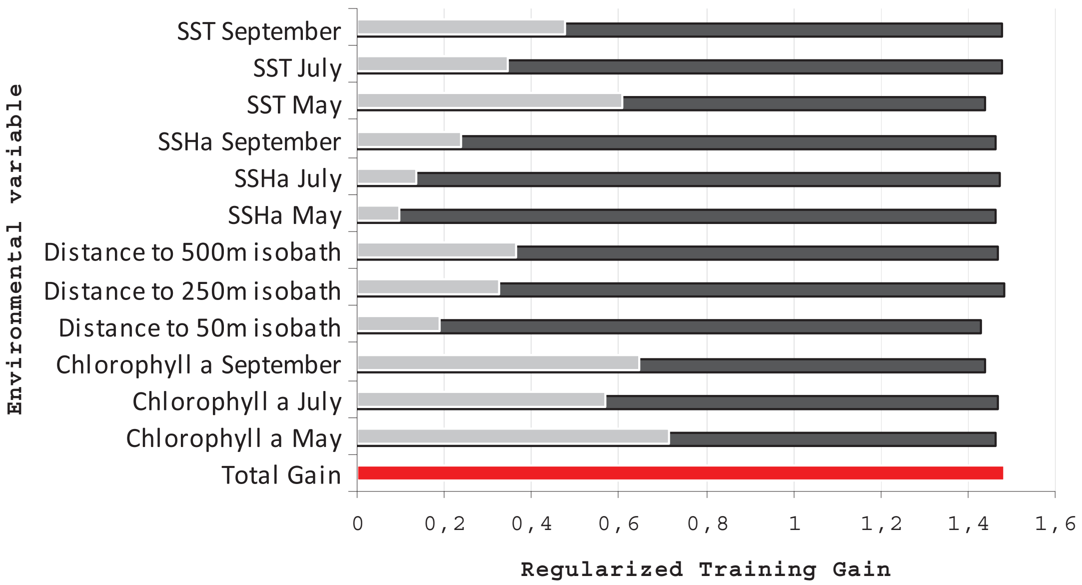

Figure 4. Plots of jack-knife test for variable importance for Maxent algorithm using all variables. The red bar indicates the gain of the model with all the variables included. Black bars indicate the gain of the model when one specific variable is removed; grey bars indicate the gain of the model with only this specific variable.

On the other hand, the gain of the model decreases when distance to the 50m isobaths is not taken into consideration (black bar lower than red bar). The distance to 500 m isobaths used by it self shows a model with considerable gain. On the other hand, the gain of the model increases when distance to 250 m isobaths is not used; therefore this variable was also taken out of subsequent runs of the model.

When *Chlorophyll a* concentration and SST from the months of July were removed from the model, the gain did not decrease. Therefore, even though the gain showed to be relatively high when these 2 variables were used in isolation, they were removed from subsequent runs of the model in order to follow the principle of parsimony (the simplest explanation is the best one).

After assessing the variable importance in the model, the most important variables appeared to be 1) *Chlorophyll a,* 2) SST at the beginning and the end of the nesting season, and 3) distance to 50 and 500m isobaths were remaining. These variables were kept for a subsequent run of the model ("a reduced model"). The results of these reduced model can be observed in Figure 5, which shows the jack-knife plot of variable importance, showing training gain of 1,596. This means that the obtained model is almost 5 times better than a random prediction (exp [1,596] =4,9).

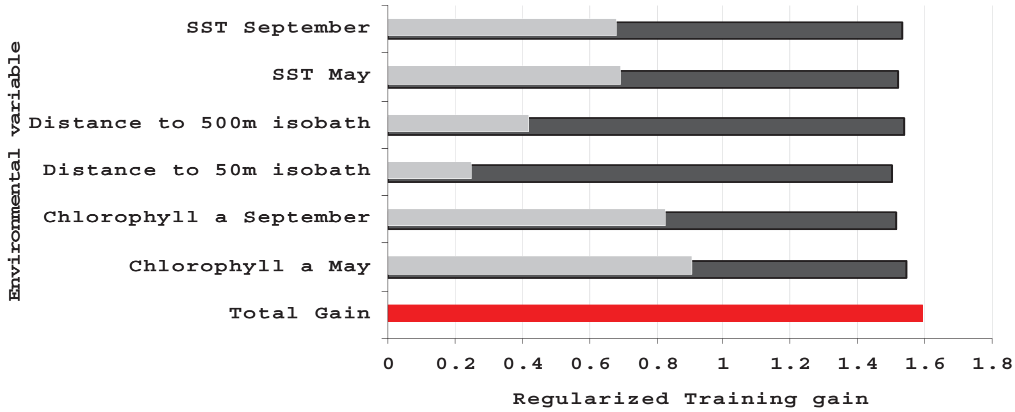

Figure 5. Plots of jack-knife test for variable importance for Maxent algorithm using a selection of most important variables. The red bar indicates the gain of the model with all the variables included. Black bars indicate the gain of the model when one specific variable is removed; grey bars indicate the gain of the model with only this specific variable.

All the variables in this reduced model contributed to the overall performance of the model. In general, if one of these variables is taken out of the model, the gain decreases (black bar becomes lower than the red bar). In addition, it seems that the conditions (*chlorophyll a* and SST) at the beginning of the season have more importance than those at the end of the nesting season.

The distance from the coast to the 50 m isobaths seems to have the most importance than the longer 500m isobaths distance when taken out of the model, nonetheless if they are used in isolation, the latter is more important.

The AUC on the ROC curve shows that the model has a very good performance, with very high values for both the test and the training data (Fig. 6). The accuracy of the model is close to 95%. In table 5, the resulting AUC for both training and test data can be observed for the 5 different partitions done with the presence sample data. Only small differences exist between the data sets, which suggests little over fitting in the Maxent predictions.

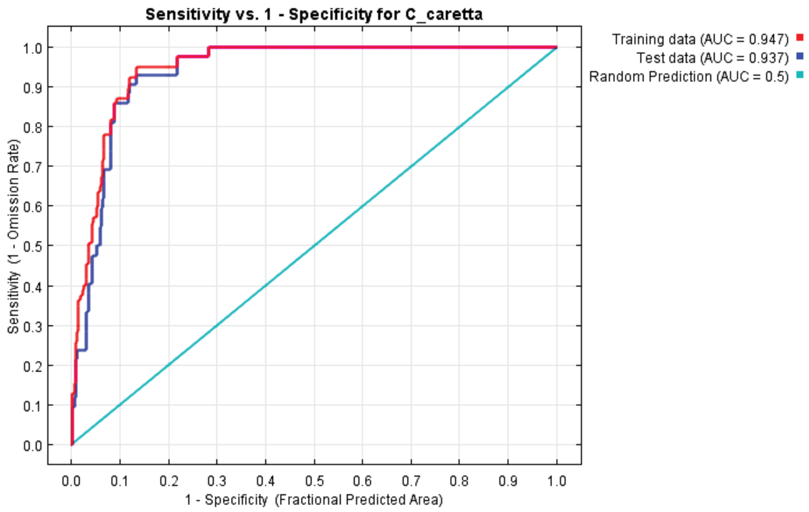

Figure 6. AUC under the ROC curve for the model using SST and Chlorophyll a from may and September, and distance to the 50m and 500m isobaths.

Table 5. Results of Area Under the ROC Curve for 5 different partitions of the presence sample data.

Partition	AUC training	AUC test	Training gain
1	0.954	0.943	1.784
2	0.947	0.937	1.674
3	0.961	0.924	1.775
4	0.954	0.932	1.584
5	0.957	0.935	1.688

3.2.3. Modelling of Mediterranean Subpopulations

In order to establish if there is a difference in the important predictor variables for the Greek and the Turkish populations (2 of the 4 that have been genetically identified in the Mediterranean), Maxent was run with the populations distinguished from each other in the samples data (MAXENT also models for more than1 species, and in this case the 2 populations were treated as 2 different species).

The results (Fig 7) indicate that there is a similar pattern when they are analyzed together or separately, with *chlorophyll a* and SST from May showing to be slightly more important than in September. Nonetheless, when comparing between the 2 populations, the Turkish population seems to be greater influenced by SST, especially from the beginning of the season.

The importance of the distance to the 50m and 500m isobaths also has a similar importance between the 2 populations, but with a minor difference. While the model gain for the Greek population decreases more when the distance to 50m isobaths is removed in a greater extent than when the distance to the 500m isobaths is removed, for the Turkish population the result is the opposite.

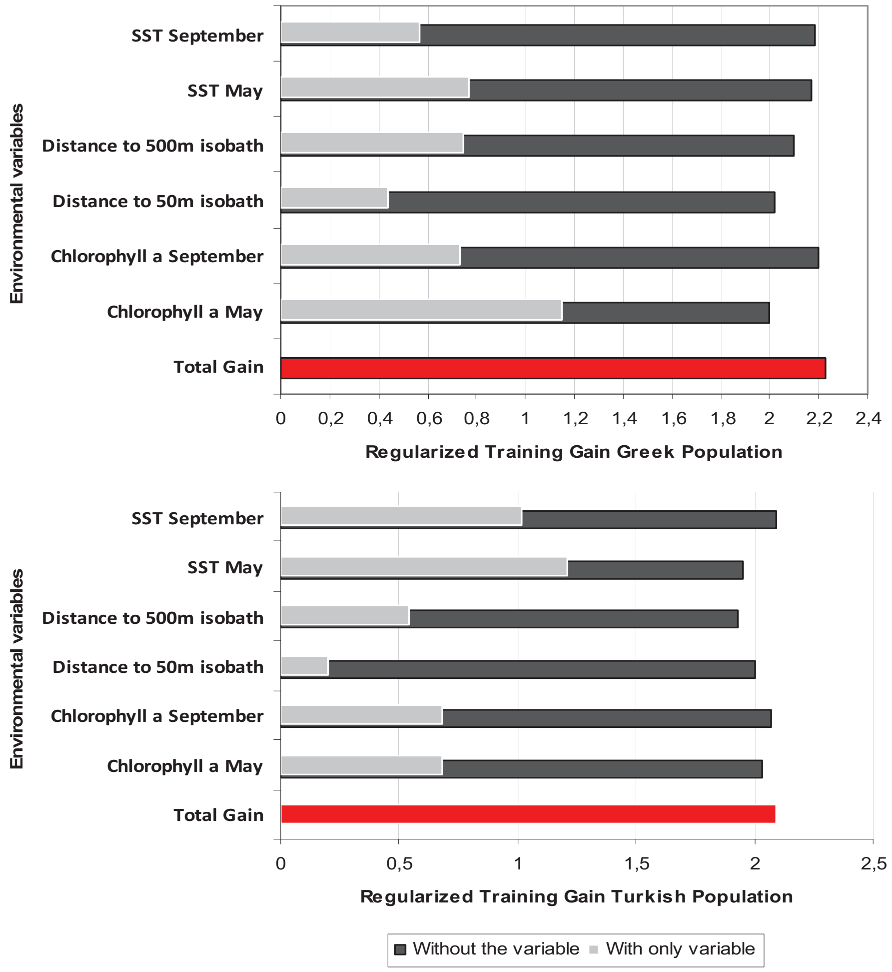

Figure 7. Plots of jack-knife test for variable importance for the Greek and the Turkish subpopulations.

Overall, the gain is greater when the model is run separately for the 2 populations than when they are joined together. Moreover, the area under the ROC curve shows that the model has a strong predictive power (Fig 8).

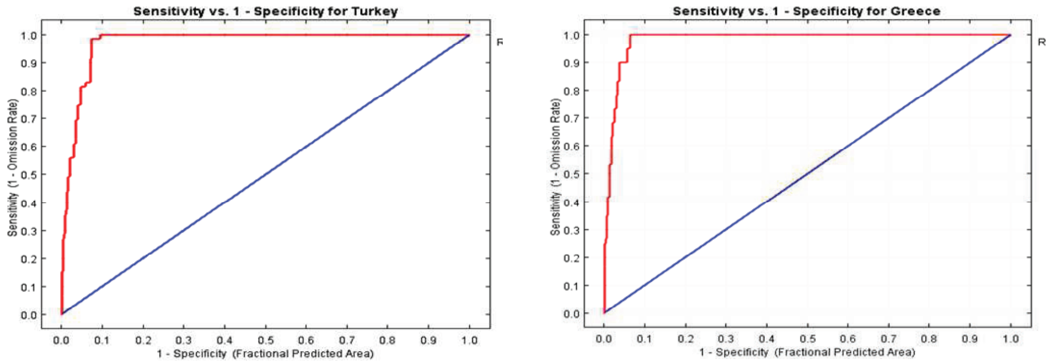

Figure 8. AUC under the ROC for the generated models for the Greek and the Turkish management units.

3.3. Relation of SST in foraging areas with nesting effort and phenology in Zakynthos.

3.3.1. Sea Surface Temperature in the foraging areas

There is a tendency of increasing mean SST in both the Adriatic Sea (r=0,627, n= 22, p= 0,002) and the Gulf of Gabès (r=0,610, n= 22, p= 0,003) in the past 21 years (Fig 9). The Adriatic is located in higher latitudes and has colder temperatures than the Gulf of Gabès (t= -28,578, df= 21, p< 0,001). Nevertheless, both sites show similar patterns though time and are highly correlated (r=0,568, n+ 22, p= 0,006).

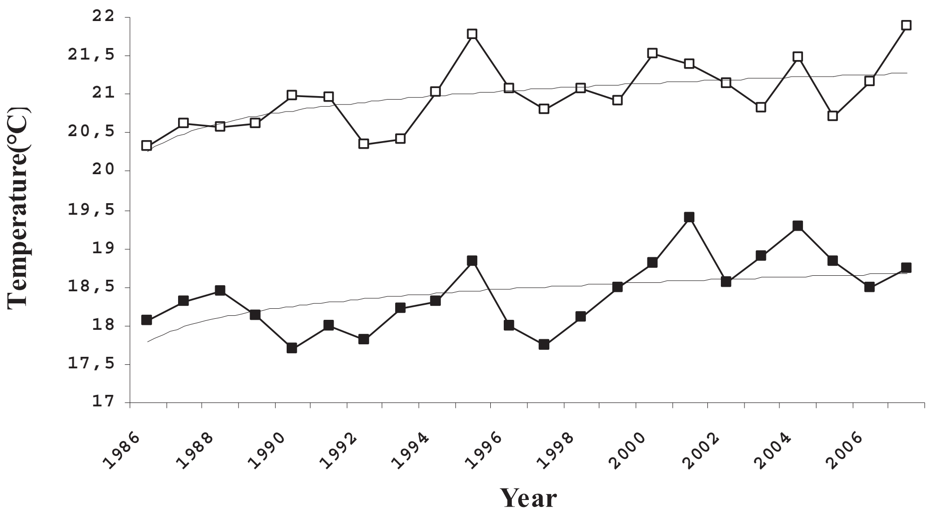

Figure 9. Temporal variability of mean SST in the Gulf of Gabès (open squares) and the Adriatic Sea (dark squares), two major foraging areas of loggerhead turtles nesting in Zakynthos Island, 1986-2007.

3.3.2. Relation SST-Total number of nests per season

The total number of nests on Zakynthos varies from one year to year (Fig 10), with a mean of 1233 ± 302 nests (minimum of 835 and a maximum of 2018).

Modelling the number of nests with 1, 2, and 3 years-lagged SST from both foraging regions resulted in a relationship (Adjusted R^2= 0,343) approaching statistical significance (F=2,565, df=19, p=0,066). Nonetheless, the best model with the less number of variables was preferred.

The resulting model indicates that 1 and 3-year lagged SST from the Adriatic Sea, and 1 and 2-year lagged SST from the Gulf of Gabès have a highly significant relationship (Adjusted R^2= 0,422; F= 10,552, df=3, p<0,001) with number of eggs laid on Zakynthos.

The number of nests increases when warmer temperatures occur in both foraging areas in the year just before the nesting season, having the SST from the Adriatic Sea a stronger influence than the Gulf of Gabès in the relationship (Fig 11a,b). On the other hand, more than 1-year lagged SST has the opposite relationship with the number of nests; the higher the SST is, the lower the number of nests (Figure 11 c,d).

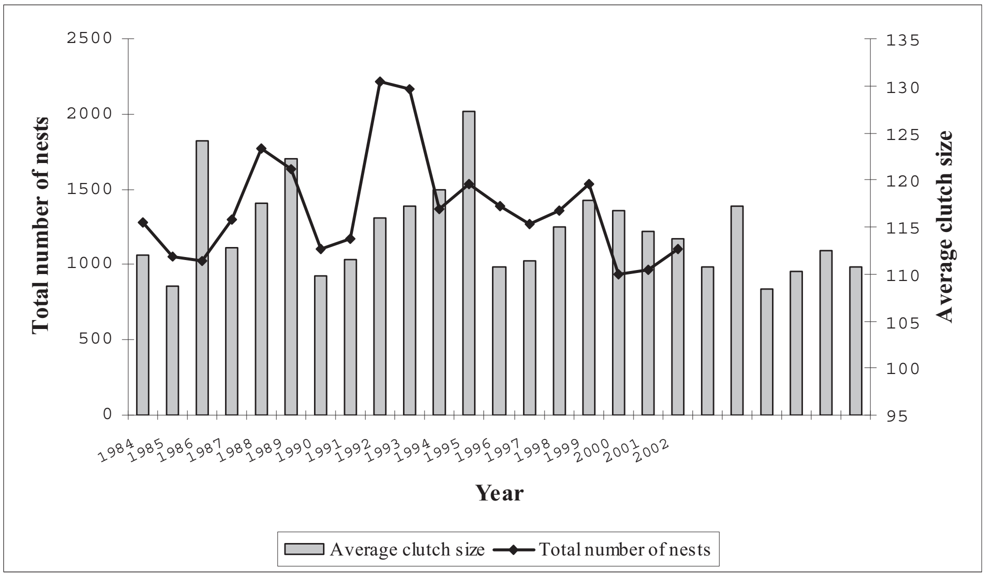

Figure 10. Total number of nests per season (1984-2002) and average clutch size (1984-2002) in Zakynthos Island, Greece. Source: Margaritoulis (2002) and Archelon (2008).

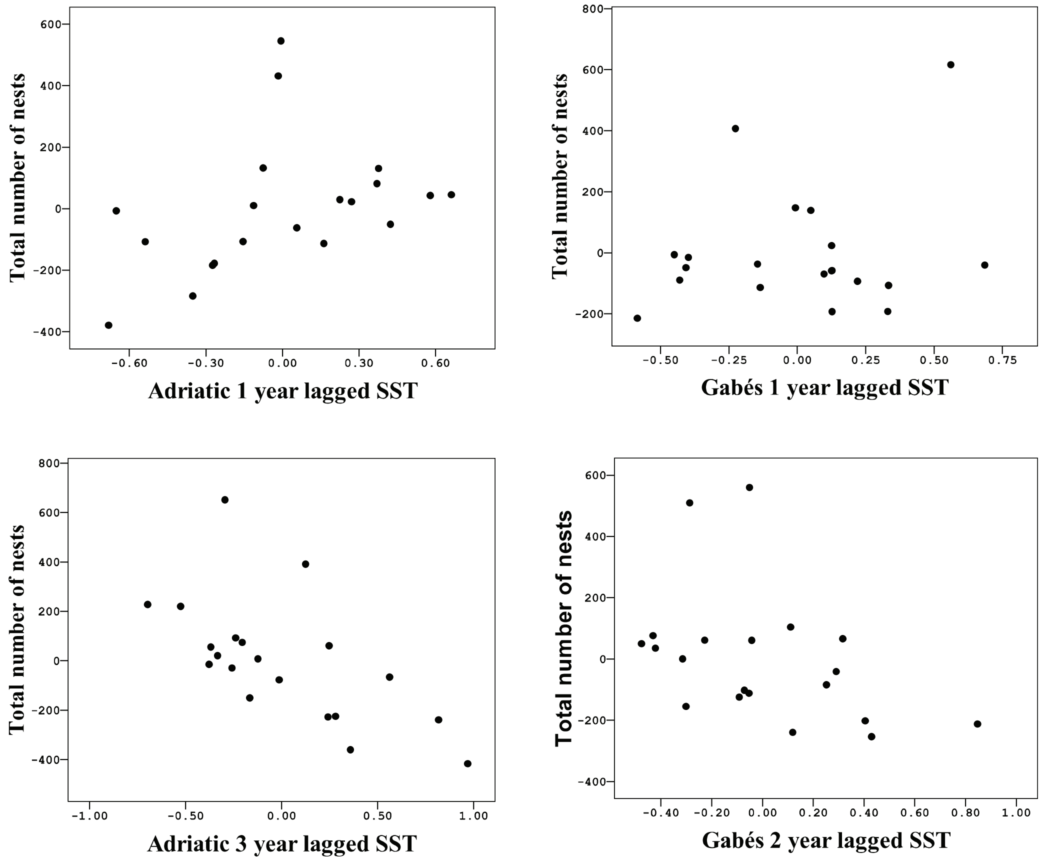

Figure 11. Partial regression plots showing the effect of adding one predictor variable (in the x axis) to a model with the other 3 variables. Response variable: total number of nests, Zakynthos, 1985-2008.

3.3.3. Relation SST-Average clutch size

The number of years in which data was available for average clutch size (average number of eggs that female loggerhead turtles) was lower than that for number of nests; nonetheless there were 17 years of data available. From this, the obtained average clutch size (Fig 10) varied per season, with a mean of 117,1 ± 5,85 eggs.

The 1 and 3-year lagged SST from both foraging areas presented a highly and significant relation with the lay in the island of Zakynthos, Greece (adjusted R^2= 0,518; F=4,757, df=14, p<0,05).

From the 4 main predictive variables, only the 1-year lagged SST from the Adriatic presented a positive correlation, which means that during years when temperature is warmer in this region, the average size of clutches laid by sea turtles increases (Fig 12a). The rest of the predictor variables have the opposite effect, with cooler temperatures being related to higher mean clutch size in Zakynthos (Fig 12 b,c,d).

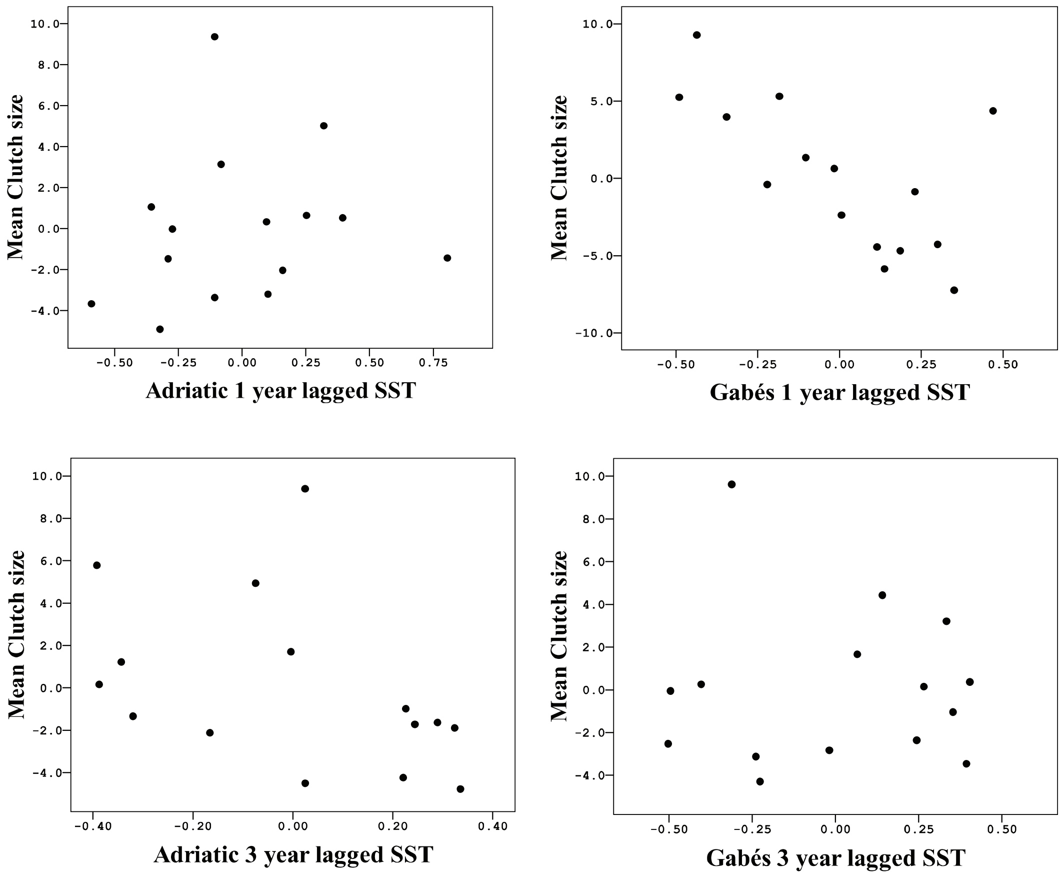

Figure 12. Partial regression plots showing the effect of adding one predictor variable (in the x axis) to a model with the other 3 variables. Response variable: mean clutch size.

3.3.4. Relation SST-nesting phenology

Three characteristics of the loggerheads nesting phenology were modelled using SST from the Adriatic Sea and the Gulf of Gabès. These 3 characteristics were: total length, first emergence of a female turtle to the beach (start of the nesting season), and last emergence of a female turtle to the beach (end of the nesting season). The phenological data was obtained for 19 years from Margaritoulis (2005), and can be observed in figure 13.

The total length of the nesting season, estimated as the period between the emergence of the first turtle attempting to nest in the year and the last emergence of a turtle attempting to nest, showed no significant correlation with lagged sea surface temperatures from the 2 foraging regions ($F= 1,352$, $df=14$, $p>0,05$).

Despite the lack of relationship between SST and the length of the nesting season, the day of the first emergence does present a strong relation (adjusted $R^2= 0,511$) with SST from the 2 foraging areas ($F=4,651$, $df=14$, $p=0,022$). In general, warmer temperatures in the foraging areas are related to an earlier start of the nesting season (Fig 14a,b,c); the exception for this is that a warmer 2-year lagged SST in the gulf of Gabès is related to a later start of the nesting season (Fig 14 d).

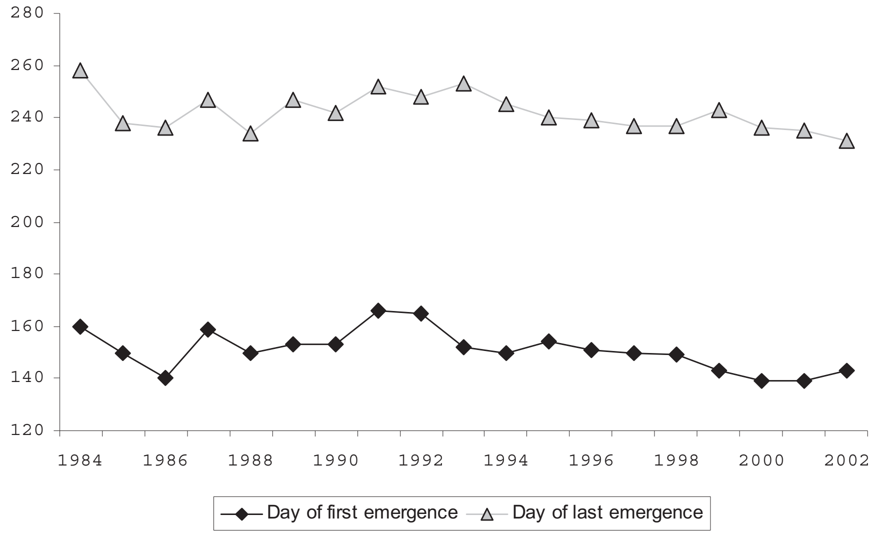

Figure 13. Days of first and last emergence of a female loggerhead turtle to the nesting beaches in Zakynthos, which marks the beginning and the end of each nesting season. Source (Margaritoulis 2005)

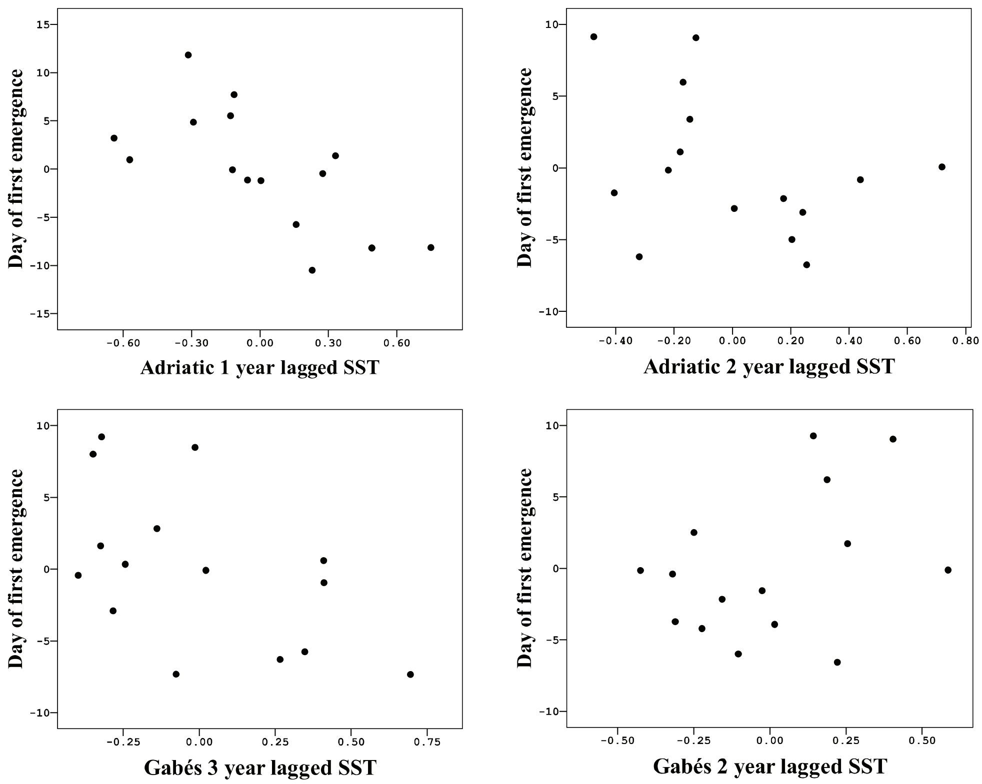

Figure 14. Partial regression plots showing the effect of adding one predictor variable (in the x axis) to a model with the other 3 variables. Response variable: first day of emergence.

Finally, warmer SST in the foraging regions are correlated (adjusted R^2= 0,511) significantly with an earlier day of end of the nesting season (F=4,271, df=14, p< 0,05). Here the model is slightly different, with 1 and 3-year lagged SST from Gabès and 2-year lagged SST from the Adriatic as the predictor variables (Fig 15).

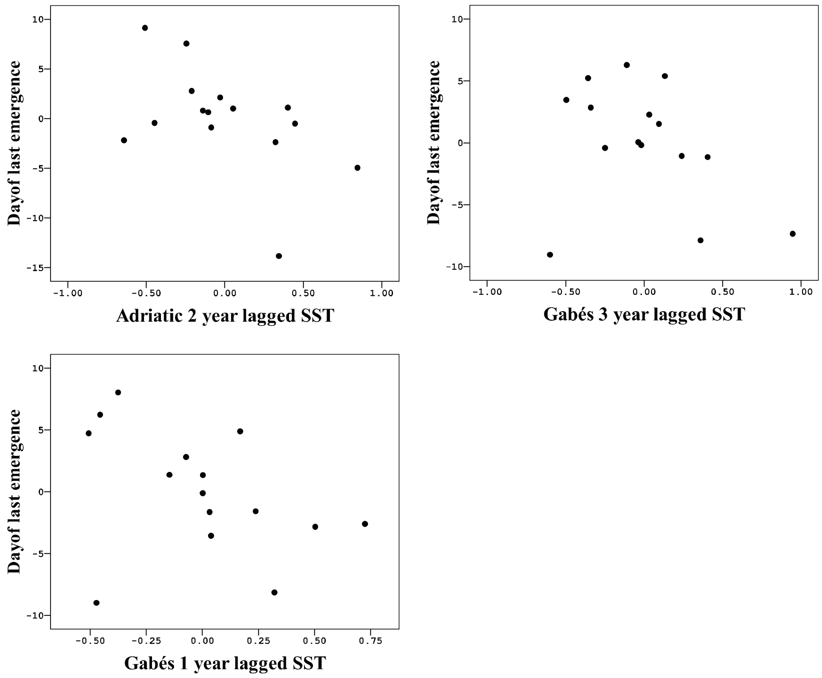

Figure 15. Partial regression plots showing the effect of adding one predictor variable (in the x axis) to a model with the other 2 variables. Response variable: last day of emergence.

4. Discussion

4.1. Improvement of a model of aquatic environment in areas where loggerhead turtles nesting in the Mediterranean Basin.

The analysis presented here confirms that SST and bathymetry are 2 characteristics of the aquatic environment that serves to predict the suitability of an area for loggerhead turtle nesting, as stated by Moin (2007). Moreover, *chlorophyll a* proved to be an important variable to add to the model. The results also suggest that the conditions at the beginning of the season have a greater weight in this suitability than those at the end of the season.

Following the recommendations given in the study mentioned above, a wider time span for the environmental variables was applied, which gives the model and the conclusions that can be drawn from it greater robustness. SST can be confirmed to be an important variable given that 23 years of data were used, instead of only two from the prior study.

4.1.1. SST and aquatic environmental suitability for nesting of female loggerheads

Ambient temperature on sea turtle nesting areas is very important for the incubation of the eggs for 2 main reasons. The first is that the sex of these animals is determined by the temperature on the second third of the incubation period (Miller, 1997). The second is that the warmer the temperature, the shorter the incubation period is; and this reduces the fitness of hatchlings (Pike, 2008b).

Sea turtles generally nest in tropical and subtropical waters. Loggerhead populations in the Mediterranean are considered to be living in the extreme of the species' thermal range, reducing the suitable period for nesting to the summer months (Schofield *et al.*, 2009). In order to exploit this months, male and female turtles mate in front of the nesting areas during April and May. Even though these months are considered cold for nesting, it ensures that females will start to nest in June when temperatures start to increase.

In this study, SST from May proved to be a very important variable in determining suitability of nesting areas. Known nesting sites have a higher mean SST (Table 3) than those areas where nesting has not been reported so far, which could result in females having higher metabolic rates (and faster egg production). The effect of this would be, in turn, that most female turtles will nest during June, July and August taking advantage of the warmer months for the incubation of the eggs.

Two other studies support what is suggested in this study that warmer temperatures are important for sea turtle nesting. Mazaris *et al.* (2008) found that with warmer mean SST in April, May and June, hatching emergence success (percentage of eggs that successfully become hatchlings and get out of the nest) increases; therefore more turtles are being produced. Schoeffield *et al.* (2009) demonstrated that even within a nesting area, female turtles follow the warmer patches of water during April and May, but drop this behaviour as the season progresses.

4.1.2. Potential predator evasion

Both shorter distances to deeper waters and lower concentrations of *chlorophyll a* in places were sea turtles nests, could be related to a strategy towards reducing the risk of hatchlings to predation. Shorter distances to deeper waters mean that less energy is used to reach safer waters.

Chlorophyll a concentration is used as an indicative of net primary productivity (NPP). Places were *Chlorophyll a* is low could result in low concentrations of phytoplankton, zooplankton and larger predators. This in turn could result in lower predation rates of hatchling turtles when reaching the water. Furthermore, adult sea turtles do not usually feed while on the breeding areas, which would explain why they do not need waters with high prey abundance.

4.1.3. Aquatic environment dynamic topography and suitability for nesting of sea turtles

Ocean currents have shown to be and important factor affecting ecology of sea turtles. Hatchlings, when reaching the water, swim towards deeper waters where apparently they take refuge in oceanic gyres. Kavvadia *et al.* (2006) and Bentivegna *et al.* (2007) found a relation between turtle migrations and currents in the Mediterranean, giving as a possible explanation the use of these in order to save energy.

For the Mediterranean Basin, there is a lack of an accurate geoid (Poulain, 1999), which still prevents an accurate computation of the ocean absolute dynamic topography, i.e. of the surface current. Therefore, SSHa deviation was used as a substitute of currents due to the lack of a good data set for this variable.

SSHa deviation was discarded from the latter stages of the modelling because apparently it has less importance than the other variables. This result should be interpreted very carefully for two main reasons. First, the resolution in which this data is obtained (approximately 25km^2) was very coarse for this study, in which aquatic environment closer to the coast was modelled. Second, as it can be seen from figure 4, this variable was taken out from the final model because it shows less importance than the other variables, not because it is not important for sea turtles.

If ocean currents data were to be used in future studies, it could be obtained from other sources than remote sensing products. In situ drifter buoy data is accurate, but the set back is that it is not always temporally available (Poulain, 1999).

Other variables such as salinity and geomagnetic fields could be a good addition when modelling suitability of a nesting area for sea turtle nesting (when only taking into account aquatic environment). It is worth noticing than in the Mediterranean, nesting is restricted to the more saline Eastern Basin. Furthermore, Asaad (unpublished data) found that salinity of the sand is higher in beaches were nesting occurs in the Island of Crete, Greece.

As with salinity, geomagnetic data had a very coarse resolution and was not suitable for this study. Nonetheless, sea turtle hatchlings have been proven to orient themselves in the ocean by the electromagnetic fields (Lohmann, 1991; Goff *et al.*, 1998).

4.1.4. Suitable aquatic environment for the populations nesting in Greece and in Turkey

The models obtained when the Turkish and the Greek populations were separated were very similar. This suggests that suitable conditions of the aquatic environment for loggerhead turtle nesting are not significantly different between them. Nevertheless, the relative importance of the environmental variables is slightly different (Fig 7). This could be reflecting the availability of different environmental characteristics in the 2 places, e.g. loggerheads using warmer waters in Turkey during May.

4.1.5. Assumptions-Limitations of the model

Besides limitations of the model mentioned in section 4.1.3., in the following 2 paragraphs we mention two assumptions that could greatly influence the outcome of the same if they are not met.

This study attempts to describe and infer which characteristics of the aquatic environment have made some places suitable for nesting of loggerhead turtles in the Mediterranean. Although this species presents less fidelity to a specific beach than others, they do not actively choose every year in which place to nest. Turtles would need a long time to adapt to changing climate, in order to find places which allow high survival rates of hatchlings.

For this reason, it is assumed for the present study, that places where loggerhead turtles are nesting in the present have had the same (or similar) environmental conditions over a period long enough for them to establish a viable nesting colony on it.

Moreover, some places where nesting is not reported in the present could have hosted populations of nesting loggerhead turtles in the past. These populations could have been vanished by human presence and exploitation, and suitable conditions of the aquatic habitat could be misrepresented in the populations that are left.

4.2. Correlation of SST with nesting effort and phenology

After analyzing the results obtained in this study, it is clear that the nesting ecology of loggerhead turtles and the SST at the areas which they use as foraging sites are related. More specifically, thermal conditions in the Gulf of Gabès and the Adriatic Sea are correlated with the reproductive behaviour of loggerhead turtles nesting on the island of Zakynthos, which represents the largest loggerhead rookery in the Mediterranean.

Such a correlation could be expected due to the ectothermic nature of reptiles such as loggerhead sea turtles. Higher temperature speeds up circulation, oxygen consumption, metabolic processes and enzyme activities, which results in an increase in food intake, but also in energetic requirements (Hochscheid *et al.*, 2004).

The relationship between a turtle's physiology and its environment (including ambient temperature) emphasizes the important role of conditions in foraging areas in influencing the ecology of these animals. Loggerhead turtles show fidelity to foraging areas in the Mediterranean, and apparently lack a seasonal latitudinal migration from colder to warmer waters (or vice versa) (Casale *et al.*, 2007). These animals spend most on their time in their feeding grounds, underlining that environmental conditions in these areas will govern their physiology, and in turn, their ecology.

Although it is clear that there is a correlation between SST and nesting ecology, the exact nature of this is not easy to elucidate. The reason is that there are 2 main foraging sites for turtles nesting on Zakynthos (one in the Adriatic, other in the Gulf of Gabès). These 2 sites have different mean SST, and there is a lagged effect of 1, 2 or more years with sea turtle nesting. Furthermore, sea turtle nesting is cyclical, occurring every 1 to 6 years (the remigration period).

4.2.1. SST-total number of nests per season

It is very interesting to observe a positive correlation between total nesting numbers in a given year and the SST the year prior to this event in both foraging areas while on the contrary; there is a negative relation with lagged SST of more than one year (Fig 11). I will deal first with the negative correlation, followed by a hypothesis of why the positive relation occurs.

Other studies have shown that colder waters are related to increased ocean productivity and prey abundance (Polovina *et al.*, 2001; Polovina *et al.*, 2006; Saba *et al.*, 2007). The results of the present study, in which colder SST in the foraging areas (3-year lagged SST from the Adriatic Sea and a 2-year lagged SST from the Gulf of Gabès) are correlated with a highest number of nests in Zakynthos, could be explained because of an increase in prey abundance, thus a higher food intake by sea turtles.

It is important to remark that Loggerhead turtles usually do not nest in consecutive years. In regular conditions, these animals require at least 1 year to acquire sufficient body fat deposits for egg formation (vitellogenesis) to occur and to sustain them on the long migrations to nesting areas (Hamman *et al.*, 2003). Average remigration of female loggerheads nesting on Zakynthos has been estimated at 2 to 3 years, which would explain why nesting numbers of loggerhead turtles in this island is correlated with SST from 2 or 3 years ago.

A possible explanation of why trends differ between the Adriatic and the Gulf of Gabès (regarding the more than a year lagged SST) is that the water in the Gulf of Gabès is on average much warmer than in the Adriatic. Loggerhead turtles are known to go through a process called overwintering, characterized by prolonged periods of inactivity at the bottom of the ocean during the coldest months of the year (Broderick *et al.*, 2007; Hochscheid *et al.*, 2007). In warmer places such as the Gulf of Gabès, this inactivity period could be shorter, allowing turtles to feed for a longer amount of time. In turn, they will acquire the necessary energy reserves for vitellogenesis faster than those overwintering in the Adriatic Sea.

Moreover, turtles have been found with full stomachs during the winter in the Gulf of Gabès, which is a sign that they do not stop feeding (Laurent & Lescure, 1994). Therefore, those sea turtles nesting on

Zakynthos that use the Gulf of Gabès as a feeding area might display shorter remigration intervals than those feeding in the Adriatic Sea, due to a higher feeding rate.

On the other hand, the fact that the relation between number of loggerhead nests increases with an increased SST in the foraging area the year prior to nesting, could seem contradictory with the result discussed above. Nonetheless, if the total input to the model from each variable is assessed, it can be observed that more than a year-lagged SST is most strongly correlated to nesting than 1 year-lagged SST (Fig 11).

Therefore, the positive relation between nest number and SST in the foraging areas could be mainly affecting turtles that have nearly reached the necessary threshold body condition for reproduction. An increase in the SST during the coldest months could extend the winter feeding period, which in turn would allow more turtles to reach this threshold.

The possibility that excellent conditions in the water might allow some turtles to nest in consecutive seasons should not be dismissed. In 8 years of monitoring turtles on Cyprus, Broderick *et al.* (Broderick *et al.*, 2007) found that about 26% of loggerheads returned to nest in consecutive years; 32% returned every 2 years and 23% returned every 3 years. Consecutive nesting seasons are unusual in sea turtles.

However, turtles that nest on Zakynthos and feed in the Adriatic or Gabès have relatively short migration routes, compared to populations such as the loggerheads nesting in Brazil, or green turtles nesting on Ascension Island (in the middle of the Atlantic). The shorter migration distances for Mediterranean loggerheads probably allow them to acquire sufficient energy for nesting more quickly than populations with long migrations.

4.2.2. SST- average clutch size

SST in the foraging areas is not only correlated with the total number of nests per season, but also with the mean clutch size (average number of eggs per nest) per season. In general, an increased in SST is related to a decrease in clutch size (Fig 12).

This is in agreement with a recent study by Mazaris *et al.* (2008), who found that April SST in Zakynthos is also negatively correlated with clutch size. April is the month when loggerhead turtles come near shore in the Mediterranean to reproduce, and so April SST is thought to be related to the nesting ecology of turtles.

Furthermore, Mazaris *et al.*(2008) found that when mean clutch sizes are higher, the number of embryos that fully develop and hatch from the eggs (hatching success) is reduced. Therefore, a possible explanation for the relation between very cold waters and high clutch size is that there has been a process in which temperatures that do not reach extremes have been selected over the extreme ones due to the higher reproductive output over season for the turtles.

Explained in other words, there is a temperature in which the relation between clutch size and hatching success is maximized, therefore each year more hatchlings are produced and reach the water. Loggerhead turtles that inhabit in the Mediterranean have been able to take advantage of this genetic plasticity, considering that they are considering to be living in the extreme of their habitat range.

In spite of what has been discussed above and the relationship between SST in foraging areas and mean clutch size is usually negative, there is a discrepancy in the results, in which at warmer temperatures in the Adriatic sea in the year prior to nesting, the higher the mean clutch size. For this reason it is hard to reach a conclusion on how the correlation between SST in foraging areas and mean size of the clutch behaves.

4.2.3. SST- nesting phenology

In this study nesting phenology of loggerhead turtles on Zakynthos showed a correlation with SST from foraging grounds, over the period 1986-2002. Several other studies have found correlations between these 2 variables (Weishampel *et al.*, 2003; Hawkes *et al.*, 2007; Mazaris *et al.*, 2008; Pike, 2008b).

There is a major difference between the above-mentioned studies and this research, which is that all the others take into account SST at the breeding sites. The present research takes into account SST at the foraging grounds. In spite of this, some similarities can be found.

First, the start of nesting activities occurs earlier in the season when temperatures are warmer (in the breeding sites in the case of the other studies and in the foraging areas in the case of this one). Nonetheless, this study also yields a very surprising result; it was expected that only the 1-year lagged SST would be correlated with the start of the nesting season, but it also yield that 2-year lagged and even 3-year lagged (in this case for the gulf of Gabès and positive) SST were correlated with the onset of the nesting season.

The rationale given in the other studies for the earlier start of the nesting season is that female turtles under warmer SST conditions can produce eggs earlier in the season. The present study suggests that there might be other underlying explanations besides this one, and that the correlation between start of the nesting season and SST is more complicated than just an earlier capacity of females to develop the eggs.

5. Conclusions

1. SST and chlorophyll a at the beginning and at the end of the nesting season, as well as the distance to the 50m and 500 m isobaths is significantly different between places were nesting of loggerhead turtles has been reported and where it has not been reported. In the areas where loggerhead turtles nest, the following situation occurs
    a. SST is significantly warmer.
    b. *Chlorophyll a* concentration is significantly lower
    c. The distance to the 50m and 500m isobaths is shorter in nesting areas.

2. SST is an important parameter when modelling the aquatic environment of areas where loggerhead turtles nest in the Mediterranean. Moin (2007) had suggested the same, nonetheless he did not used an appropriate time span of SST data (only 2 different years); this study used a data set comprising 23 years of SST records and what was suggested by Moin is confirmed.

3. Chlorophyll a is an important parameter in the determination of the suitability of the aquatic environment of a coast for sea turtle nesting in the Mediterranean basin. This parameter could help to better explain why sea turtle only nest in specific areas.

4. It is not clear from the present study on how different the importance of variables is on determining suitability of the aquatic environment for the populations nesting in Greece and in Turkey.

5. The total number of nests is positively correlated with the SST from the Adriatic Sea and the Gulf of Gabès the year prior to the summer nesting in the Island of Zakynthos, Greece. On the contrary, it is negatively correlated with more than 1-year lagged SST.

6. The average clutch size per year laid by female loggerhead turtles in the island of Zakynthos presents a positive correlation with a 1-year lagged SST from the Adriatic Sea, but a negative correlation with a 1-year lagged SST from the Gulf of Gabès and 3-lagged SST from both places.

7. There is no correlation between the length of the nesting season of loggerhead turtles nesting in Zakynthos and the average SST in the Adriatic Sea and the Gulf of Gabès, 2 of the foraging areas of these individuals. In spite of this, there is a correlation between these SST and the start and the end dates of the nesting.

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6. Appendices

Appendix A: *C caretta* nesting sites in the Mediterranean used for analysis in this study.
Data compiled by Moin (2007). For more information on data sources refer to the mentioned study.

Site	Country	Longitude	Latitude	Nest Density	Total nests
Akrotiri	Cyprus	32.874898	34.60373	2	23
Alagadi	Turkey	33.477552	35.387797	31	100
Anamur	Turkey	33.914926	36.216107	14	1910
Belek	Turkey	31.065993	36.805666	19	130
Bengasi	Lybia	20.024548	32.375352	8	160
Chania	Greece	23.900781	35.565773	8	115
Chrysochou	Cyprus	32.44892	35.127521	8	120
Dalaman	Turkey	28.747114	36.646972	8	73
Dalyan	Turkey	28.568905	36.716016	51	165
Demirtas	Turkey	32.150086	36.365073	10	98
Ekincik	Turkey	28.532975	36.746067	20	20
El Mansouri	Lebanon	35.148813	33.216271	26	12
Fethiye	Turkey	28.998713	36.639427	13	124
Gazipaza	Turkey	32.24577	36.239841	2	110
Goksu	Turkey	32.89166	36.011379	3	65
Great Kuriat	Tunisia	11.039009	35.783773	13	12
Gulf o Sirte	Lybia	17.649186	31.19911	8	160
Kale	Turkey	30.056746	36.195325	12	39
Kizilot	Turkey	31.552904	36.660912	11	107
Koroni	Greece	21.976588	36.769113	20	55
Kotichy	Greece	21.251073	38.015575	10	50
Kouf NP	Lybia	23.975328	32.400206	8	160
Kumluca	Turkey	30.272068	36.256327	11	163
Kyparissia	Greece	21.661085	37.304192	62	581
Lakonikos	Greece	22.688245	36.753193	13	192
Lybia	Lybia	19.777692	31.11539	8	160
Lybia N	Lybia	19.121823	30.560211	8	160
Messara	Greece	24.701436	35.032842	5	54
Nof Kefalos	Greece	26.983289	36.799276	15	60
Patara	Turkey	29.258608	36.22895	100	53
Rhodes	Greece	27.845188	35.895444	2	11
Rethymo	Greece	24.547475	35.426239	30	387
Tekirova	Turkey	30.579444	36.467437	1	1
Zakynthos	Greece	20.906104	37.692688	236	1301

Appendix B. Criteria for assigning weights to loggerhead turtle nesting areas according to nesting density.

Nest density	Assigned number of sample points
1-2	1
3-5	2
6-10	3
11-20	4
21-40	5
41-75	6
76-100	7
236	10