

Update of the Loggerhead Sea Turtle (*Caretta caretta*) Population Nesting in Koroni, Greece, Mediterranean

Dimitris Margaritoulis^{1,*}, Gonçalo Lourenço¹, and ALan F. Rees¹

¹ARCHELON, the Sea Turtle Protection Society of Greece, Solomou 57, GR-104 32 Athens, Greece.

*Correspondence: E-mail: margaritoulis@archelon.gr (Margaritoulis)

E-mail: alanrees@gmail.com (Rees); goncalo.j.lourenco@gmail.com (Lourenço)

Received 1 March 2023 / Accepted 4 August 2023 / Published 5 October 2023

Communicated by Yoko Nozawa

Long-term monitoring programs are valuable in assessing population trends and evaluating conservation status especially for threatened species exhibiting delayed maturity such as marine turtles. The loggerhead sea turtle *Caretta caretta* is a globally distributed species with a regional population within the Mediterranean Sea. Loggerhead nesting in the Mediterranean occurs mainly in the eastern basin, with nesting areas classified as per their magnitude and density. A “moderate-dense” nesting area in Greece is the 2.7 km Koroni beach which has been monitored by ARCHELON since 1995 with the aim to collect reproductive data and to protect nests. Data collected over 25 years showed an average annual number of 55.8 nests, a nesting success (percentage of emergences resulting in egg-laying) of 38.0% and a nesting density of 20.7 nests/km. Nest numbers exhibited a significantly increasing trend in recent years, while clutch size showed a significant downward trend. Incubation durations, considered to be an indicator of incubation temperature and subsequently hatchling sex ratio, have been significantly decreasing over the years—a possible sign of global warming. A major threat is nest predation by foxes and dogs, which has been effectively controlled through the fencing of nests. This nesting population, despite its moderate size, may contribute to the genetic homogeneity of the larger western and eastern nesting aggregations of loggerhead turtles in Greece. The nesting beach has been recently included in the European Union’s NATURA 2000 network of protected areas. Continuation of this long-term monitoring program is expected to provide further insights into the reproductive traits of this important loggerhead population.

Key words: Climate change, Conservation, Population trend, Predation, Monitoring

BACKGROUND

The loggerhead sea turtle (*Caretta caretta*) is a cosmopolitan species with mainly subtropical and temperate distribution across the oceans (Dodd 1988). Major nesting aggregations are reported in the Atlantic Ocean (Cabo Verde, southeastern USA, Brazil), Indian Ocean (Oman, South Africa), Pacific Ocean (Australia, Japan), and Mediterranean Sea (Dodd 1988; Willson et al. 2020; Hays et al. 2022). Synthesizing ecological, genetic and biogeographical information, Wallace et al.

(2010) identified ten Management Units for this species globally, one of which encompassed the populations breeding in the Mediterranean. Loggerheads in the Mediterranean nest mainly in its eastern basin with major rookeries in Greece, Turkey, Libya and Cyprus (Margaritoulis et al. 2003; Casale and Margaritoulis 2010). These four countries contain about 96% of all documented loggerhead nests in the Mediterranean, with Greece alone holding about 46% (Casale et al. 2018).

The Greek coasts of the Ionian Sea, including the Ionian Islands, feature moderate to major loggerhead

nesting aggregations (*sensu* Margaritoulis 2000), with two of them at Laganas Bay on Zakynthos Island and at Kyparissia Bay in western Peloponnese, being the largest in the Mediterranean (Margaritoulis et al. 2003; Casale et al. 2018). A nesting site with moderate nesting (*i.e.*, with mean annual number of nests between 20 and 100; Margaritoulis 2000) is that of Zaga-Memi beach near the town of Koroni (called Koroni beach from hereon) in the southern Peloponnese. This beach has been monitored by ARCHELON, the Sea Turtle Protection Society of Greece, since 1995. The first data on annual nest numbers were published by Margaritoulis (2000) and Margaritoulis et al. (2003), and the main reproductive parameters and associated threats for the period 1995–2002, were included in Margaritoulis and Rees (2006). Nesting data of the 2003 season were presented by Bazigou et al. (2004). Egg predation by foxes and dogs has been recognized as a major threat to the loggerhead population breeding in Koroni (Margaritoulis and Rees 2006).

Presenting up-to-date nesting data of loggerhead turtles would support conservation status evaluations (*e.g.*, Mazaris et al. 2017; Casale et al. 2018), including the IUCN’s Red Listings (Casale et al. 2018), the

European Union’s (EU) Marine Strategy Framework Directive (2008/56/EC), where the loggerhead turtle is an “indicator” species for biological diversity, and the Integrated Monitoring and Assessment Program of the Barcelona Convention (Decision IG.22/7). Further, the evolution of some reproductive traits over time would provide indications of the extent of climate change effects (Patel et al. 2016). In this article we analyze all available data until 2021 and examine annual nest numbers, key reproductive parameters, and the evolving rates of nest predation over time.

MATERIALS AND METHODS

Study site

Koroni beach has a length of 2.7 km, a varying width of 5–32 m, and is located at the southwestern peninsula of the Peloponnese, from about 36.779°N, 21.935°E to 36.794°N, 21.960°E (Fig. 1). The beach has a southeastern orientation, consists of fine to medium grained sand with pebbles at places and is generally backed by native vegetation, cultivated fields and

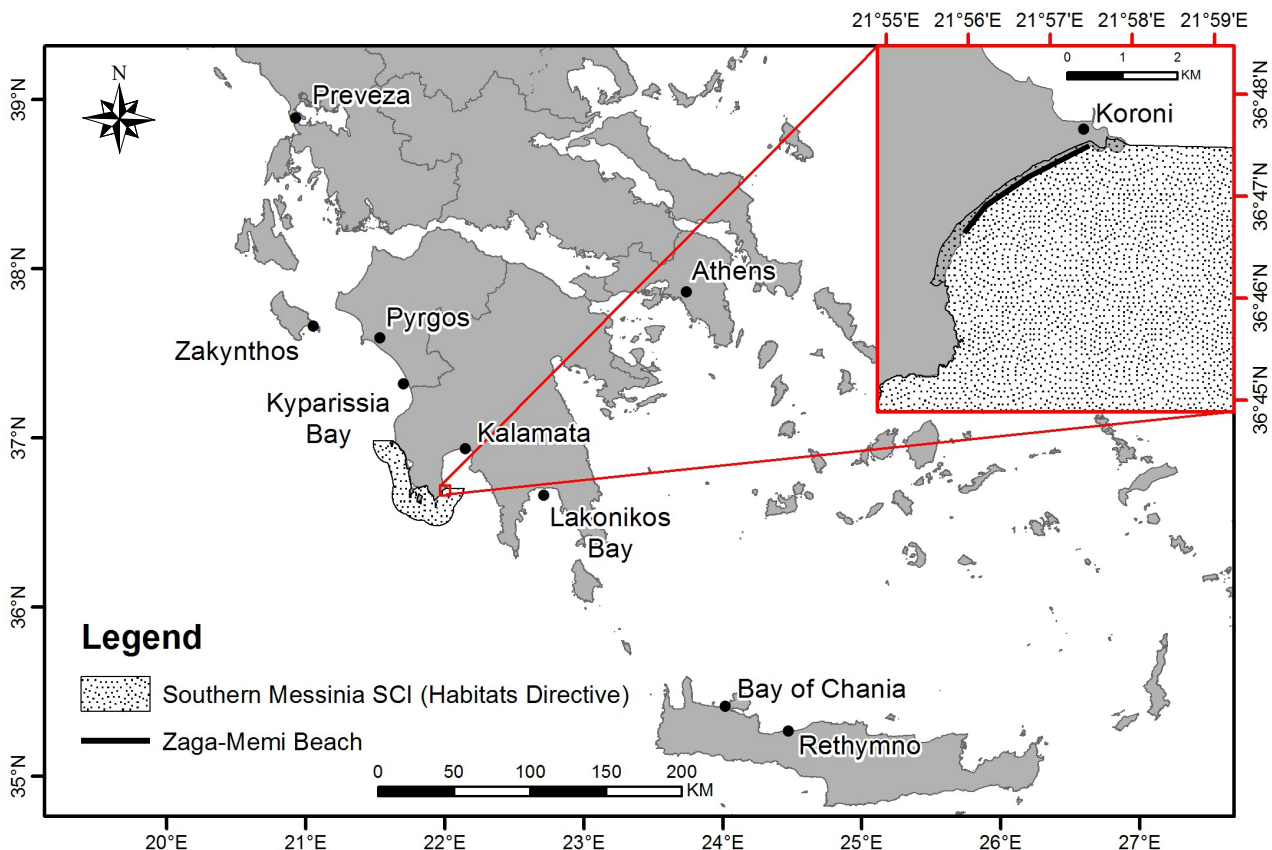


Fig. 1. Map of southern Greece showing the location of Koroni beach (Zaga-Memi beach) and the associated NATURA 2000 site GR2550010 (Marine area of southern Messinia SCI) as well as localities referred in the text.

occasional buildings (Fig. 2). Due to the proximity of the town of Koroni and a road that reaches the beach's westernmost section, parts of the beach are frequented during the summer by visitors, who use a moderate level of beach furniture and access a wind-surf rental facility. The climate is largely seasonal, with high temperatures and low precipitation during the summer, while autumn and winter are characterized by increased precipitation, occasional storms, and lower temperatures.

Field methods

Fieldwork was carried out by trained volunteers following standard protocols and supervised by experienced field assistants. The beach was surveyed, on foot, and adult female turtle tracks (“emergences”) were counted, evaluated and classified as “nesting” or “non-nesting”. Nesting success was defined as the percentage of emergences resulting in egg-laying. Egg chambers were manually excavated until the uppermost eggs became visible. Nests were marked and monitored until emergence of hatchlings or until 70 days of incubation. To mitigate nest predation by foxes and dogs, flat metal grids were positioned over nests to varying extent over the seasons, depending on availability of materials and



Fig. 2. Photo of Koroni beach towards southwest (Photo: Dimitris Margaritoulis/ ARCHELON).

human resources. Grids were anchored in the sand with bamboo sticks.

A nest was defined as predated when predators had reached the eggs. The recording of predation rates (percentage of predated nests to total nests) started in 1997. Some nests were relocated higher on the beach within 12 hours of egg-laying to avoid inundation by the sea. Since 1996 (with the exception of 2001 when no excavations were conducted), the practice of excavating nests that had either hatched or remained unhatched for 70 days after egg-laying had been undertaken. This approach aimed to evaluate clutch size (the number of yolked eggs within a clutch), hatching success (the percentage of eggs that hatched) and the rate of hatchling emergence success (the percentage of eggs that produced hatchlings that made it to the beach surface). The incubation duration (the number of elapsed days from egg-laying until the emergence of the first hatchling at the beach surface) of hatched nests had been recorded since 1996. Hatching success, hatchling emergence success and incubation duration were calculated for non-relocated, non-inundated and non-depredated nests, while clutch size was assessed from excavation of non-depredated nests. Field work was not carried out in 2009, due to logistical considerations, nor in 2020, due to pandemic restrictions.

Statistical analysis

To examine the trend of the annual nest numbers, we used a Generalized Additive Model (GAM), as it better fits the non-linearity of the data. In examining trends in hatching success, hatchling emergence success, clutch size and incubation duration, we used linear models since these data were both linear and normally distributed (Shapiro-Wilk normality test, $p > 0.05$). All analyses were produced using R (R Core Team 2020) and RStudio (RStudio IDE 2022).

RESULTS

In the period 1995–2021, the annual number of nests ranged from 29 to 134 with a mean of 55.8 ± 25.9 nests (median: 49 nests), and the annual nesting success varied from 24.0% to 55.6% with an overall mean of 38.0% (Table 1). The Coefficient of Variation (CV; defined as $SD/mean$) for nests, indicating inter-annual variability, was 0.46. Nesting density ranged from 10.7 to 49.6 nests/km/year (mean = 20.7 nests/km/year, median = 18.1 nests/km/year, $n = 25$ years) (Table 1). Annual nest numbers were gradually decreasing until about 2012 but then started to increase, showing a significant overall increasing trend ($R^2 = 0.7403$,

$F = 12.35, p < 0.001$) (Fig. 3).

The mean annual clutch size was 105.0 eggs (range = 84.2–122.1 eggs, median = 107.4 eggs, $n = 23$ years) (Table 1). A significantly decreasing trend was recorded in the annual mean value for clutch size ($R^2 = 0.5708, t = -5.285, p < 0.001$) (Fig. 4). Mean annual hatching success was 76.3% (range = 60.4–87.0%, $n = 23$ years) and hatchling emergence success was 67.3% (range = 54.6–78.1%, $n = 23$ years) (Table 1), with non-significant trends over the years. The mean annual incubation duration ranged from 46.8 to 54.0 days with an overall mean of 50.1 ± 2.1 days (median = 49.8 days) (Table 1). Annual incubation durations showed a significant decreasing trend over time ($R^2 = 0.5211,$

$t = -4.892, p < 0.001$) (Fig. 5).

The most common problem affecting hatchling recruitment in Koroni is nest predation by foxes and dogs, which dig up nests and take eggs and hatchlings. Since 1997, when we started to monitor nest predation, 0–53 nests were predated per season (mean = 14.1 nests/season, median = 12 nests/season, $n = 23$ years) (Table 1) despite the application of metal grids over nests. Annual predation rates varied from 0% to 64.9% (Table 1, Fig. 6) with a mean of 23.2%. The highest predation rate (64.9%) occurred in the year 2000 when, because of a lack of resources, nest protection measures were seriously reduced. The predation rate over the years does not show any remarkable trend ($R^2 = 0.262, F = 1.509,$

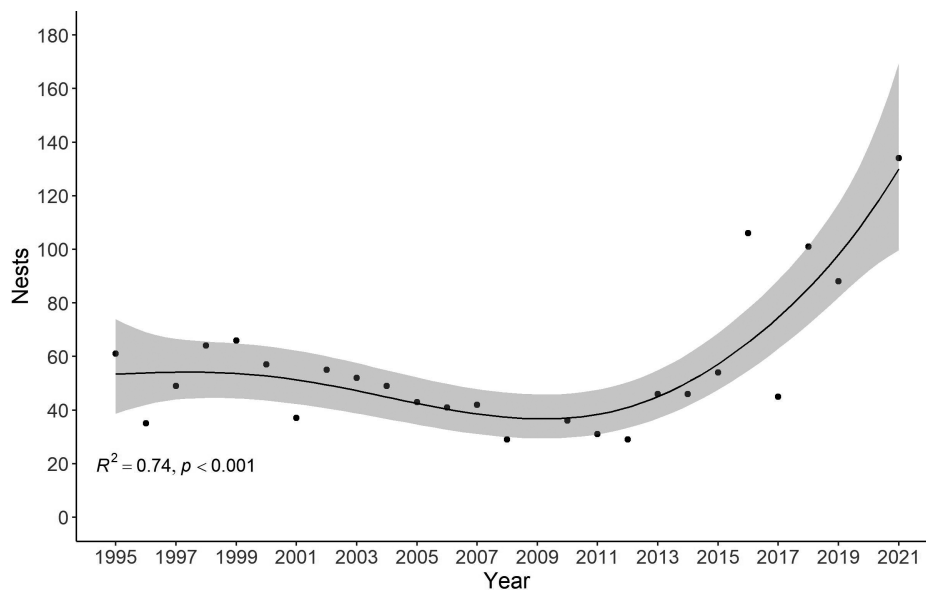


Fig. 3. Trend of the annual number of nests in Koroni for the period 1995–2021. No fieldwork was conducted in the years 2009 and 2020. Plot fitted with GAM for Poisson distribution with overdispersion (Quasipoisson). Grey band represents the 95% confidence interval for the fitted model.

Table 1. Reproductive parameters of the loggerhead population nesting in Koroni beach over the period 1995–2021 (except for the years 2009 and 2020, when no work was carried out). No data for clutch size, hatching success and hatchling emergence success for year 2001

Reproductive parameter	Annual mean	Range of annual means	n (years)	n (clutches)
Number of emergences	147.0	76–273	25	n/a
Number of nests	55.8	29–134	25	n/a
Nesting success (%)	38.0	24.0–55.6	25	n/a
Nesting density (nests/km)	20.7	10.7–49.6	25	n/a
Number of predated nests	14.1	0–53	23	n/a
Rate of predation (%)	23.2	0.0–64.9	23	n/a
Clutch size (eggs)	105.0	84.2–122.1	23	661
Hatching success (%)	76.3	60.4–87.0	23	565
Hatchling emergence success (%)	67.3	54.6–78.1	23	565
Incubation duration (days)	50.1	46.8–54.0	24	558

$p = 0.246$). Most predated nests, protected with a grid, were invaded by predators through tunneling under the grid (Fig. 7).

DISCUSSION

Although Koroni beach, hosting on average less than 100 nests per season, was classified as an area of

“moderate” nesting (*sensu* Margaritoulis 2000), its mean annual nesting density (20.7 nests/km) is larger than densities reported for some “major” nesting areas in Greece; *e.g.*, Lakonikos Bay (7.3 nests/km) and Bay of Chania (8.9 nests/km) (Margaritoulis 2000). In a more detailed classification of loggerhead nesting beaches in the Mediterranean, Koroni beach is characterized as an area of “moderate-dense” nesting (*i.e.*, 20–99 nests/year, ≥ 6.5 nests/km/season; Casale et al. 2018).

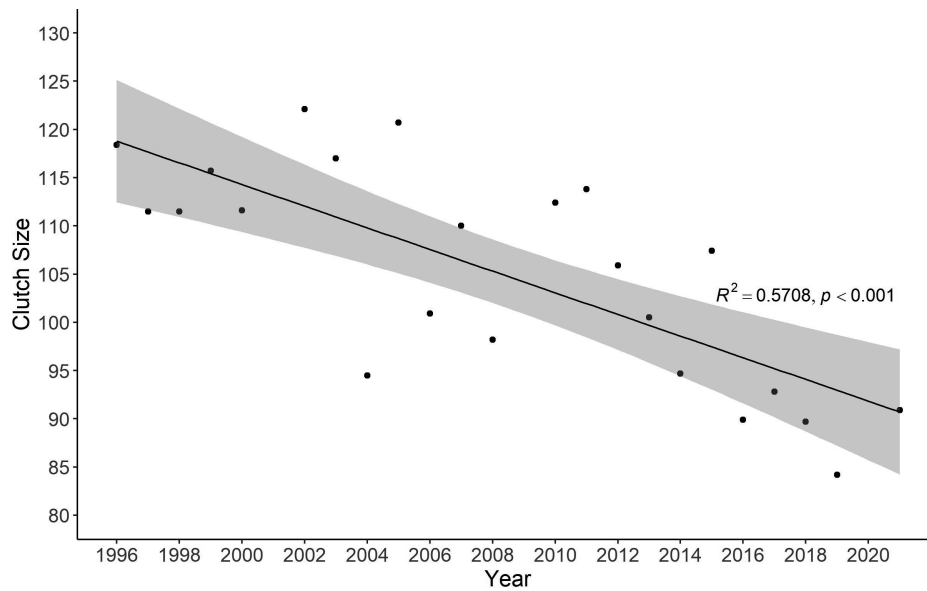


Fig. 4. Trend of the annual mean clutch size in Koroni for the period 1996–2021. No clutch size measurements in 2001 and no fieldwork conducted in years 2009 and 2020. The linear model demonstrates a significant decline in clutch size over the years. Grey band represents the 95%.

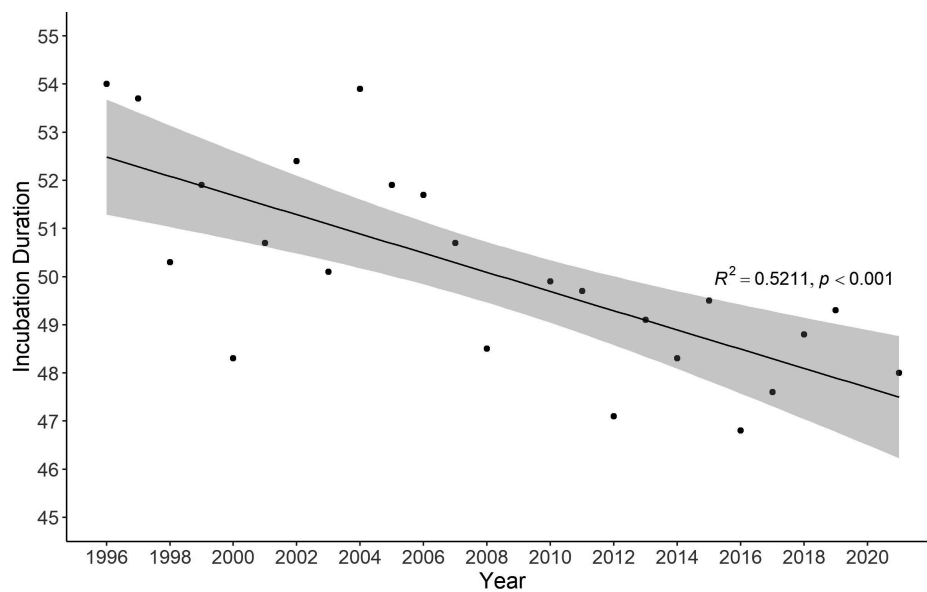


Fig. 5. Trend of the annual mean incubation duration in Koroni for the period 1996–2021. No fieldwork conducted in the years 2009 and 2020. The linear model demonstrates a significant decline of the incubation duration over the years. Grey band represents the 95% confidence interval for the fitted model. All mean annual values are below the pivotal incubation duration for Greece (56.6 days), assessed by Mrosovsky et al. (2002).

Increasing trends of nest numbers have also been reported in recent years in other nesting areas of Greece (*e.g.*, Zakynthos (Margaritoulis et al. 2022), Romanos (Teneketzis and Margaritoulis 2019)), and the Mediterranean (Casale et al. 2018; Sönmez et al. 2021). However, these positive trends originate from long-term monitoring programs which may have benefited from site-specific protection measures and conservation actions and hence, may not be entirely representative (Casale et al. 2018).

Inter-annual variability of loggerhead nesting in Koroni (CV = 0.46) is considered to be high compared to other areas in Greece, *e.g.*, Zakynthos (CV = 0.26; Margaritoulis et al. 2022), and in the Mediterranean (Broderick et al. 2001). Female loggerhead turtles generally do not breed every year, but rather only when they can accumulate the necessary energy reserves to support their reproductive migration to nesting areas (Schroeder et al. 2003). Remigration intervals may vary from one to nine years depending on environmental factors and food resources (Dodd 1988). Hence, the noted high inter-annual fluctuations in the number of nests in Koroni may have been caused by the turtles' complex reproductive traits originating from factors at the foraging areas (Broderick et al. 2001; Pike 2013).

Koroni has the highest long-term nesting success rate (38.0% over 25 seasons) in Greece, surpassing other locations such as Zakynthos with 26.2% over 38 years (Margaritoulis et al. 2022), and Kyparissia Bay with 34.6% over 9 years (Margaritoulis and Rees 2001; Rees et al. 2002; Margaritoulis and Rees 2003).

In the Mediterranean, the highest long-term nesting success for loggerheads was 48.8% over the 9-year period 2013–2021 at Çıralı beach, Turkey (Sönmez et al. 2021; Elginöz et al. 2022). Even higher nesting successes were reported outside the Mediterranean, *e.g.*, in Oman (mean 71% over 9 years; Willson et al. 2020) and in Florida (mean 50% over 11 years; Weishampel et al. 2003). High nesting success indicates generally limited anthropogenic disturbances and favourable environmental conditions, which enable nest digging and egg-laying (Miller et al. 2003).

The range of annual mean clutch sizes in Koroni (84.2–122.1 eggs) was a little below the range of the loggerhead population nesting in Zakynthos resulting from a 38-year dataset (92.7–130.4 eggs; Margaritoulis et al. 2022). Notably, the clutch size of loggerheads in Greece is the largest in the Mediterranean because of their large body size (Margaritoulis et al. 2003; Casale et al. 2018); these two variables are strongly inter-related (Tiwari and Bjorndal 2000; Broderick et al. 2003; Zbinden et al. 2011). The significantly decreasing trend of clutch size in Koroni resembles a similar trend reported for Zakynthos turtles which was explained by their decreasing body size over time (Margaritoulis et al. 2022). Regrettably, we have no body size data for turtles nesting in Koroni to verify this. It is worth noting that decreasing trends of body size and of clutch size have also been observed in other breeding areas worldwide and for other sea turtle species (*e.g.*, Le Gouvello et al. 2020; Phillips et al. 2021; Mortimer et al. 2022) providing an indication that this global phenomenon

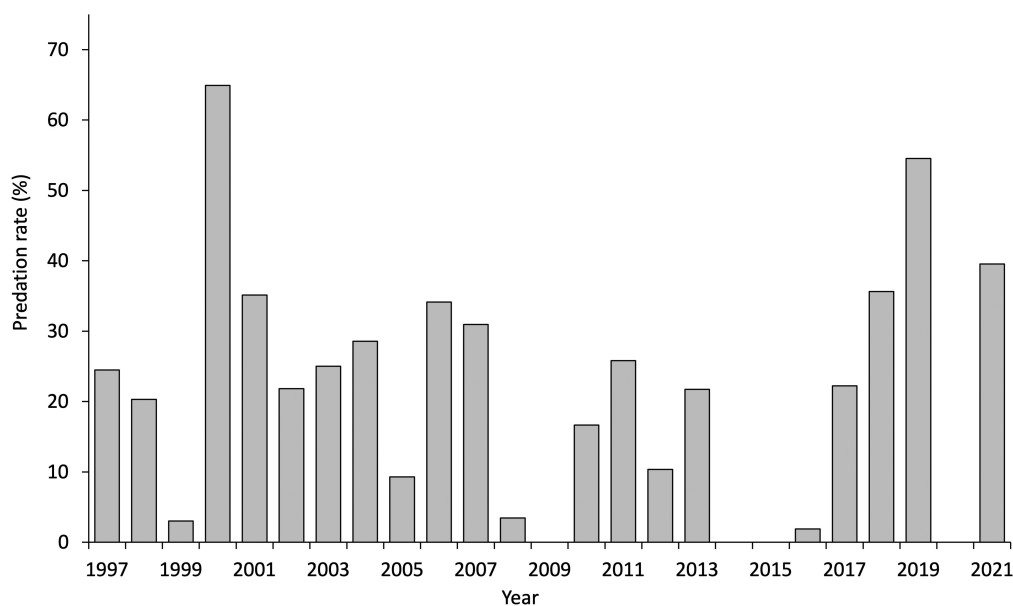


Fig. 6. Predation rates of Koroni nests for the period 1997–2021. No fieldwork conducted in years 2009 and 2020. No predation events in years 2014 and 2015.

is probably a result of climate change affecting turtles' food resources at their foraging areas (Hays et al. 2022).

Values of hatching success, hatchling emergence success, and incubation duration lie generally within the range reported for loggerhead turtles in other nesting areas of Greece (Margaritoulis 1988; Margaritoulis et al. 2003; Teneketzis and Margaritoulis 2019; Margaritoulis et al. 2022) and the Mediterranean (Margaritoulis et al. 2003; Casale et al. 2018), as well as in loggerhead nesting areas outside the Mediterranean (Dodd 1988; Miller et al. 2003). All above comparisons of reproductive traits suggest that loggerheads in Koroni comprise a healthy and viable population.

Marine turtles exhibit temperature-dependent sex determination, with female hatchlings being produced at higher incubation temperatures (Mrosovsky and Yntema 1980). The incubation duration can be used as a proxy of incubation temperature, with long incubations indicating low temperatures and producing more male hatchlings, and with short incubations signaling more female hatchlings (Mrosovsky et al. 1999). The “pivotal” temperature, which produces 50% female hatchlings, and the associated “pivotal” incubation duration were assessed for Greece to 29.3°C and to 56.6 days respectively (Mrosovsky et al. 2002). In Koroni, all annual values of incubation durations were

below the pivotal incubation duration of 56.6 days, leading to the presumption that the hatchling sex ratio was female biased. The significant decrease of the incubation durations over time indicates a continuing increase of the incubation temperature, a potential effect of global warming, and hence a continuing increase of the proportion of female hatchlings (Mrosovsky et al. 2002). In short, the primary sex ratio of loggerhead turtles in Koroni is predominantly female, and this feminization is growing possibly due to global warming. The growing feminization of hatchlings may explain, to a certain degree, the increase in nest numbers noted in Koroni. Indeed, more female hatchlings would result in more female turtles and hence more nests per season, as reported in other nesting areas experiencing increases in nest numbers (*e.g.*, Laloč et al. 2014; Hays et al. 2022).

The natural nest predation rate (*i.e.*, without protection measures) at Koroni, that is likely to be more than 60%, as found in 2000 when little nest protection was undertaken, is similar to that found in Turkey (Dalyan beach: 62.5%; Yerli et al. 1997) and higher than that found at the major nesting area of Kyparissia Bay, where predation rates of 48.4% and 48.8% were recorded in 1987 (Margaritoulis 1988) and 1994 (Margaritoulis et al. 1996) respectively. Hence, nest protection through the use of grids in Koroni is seen to be an effective way of reducing predation and increasing hatchling production, as reported also in Turkey (Başkale and Kaska 2005). The extreme annual fluctuations of predation rates may be attributed to seasonal changes in the predators' populations or activity. Further, it is known that excess humidity or rain increases the clumping of sand which facilitates predators to tunnel under the grids. These stochastic environmental conditions can further contribute to the recorded large variation of predation rates.

The nesting habitat at Koroni, despite the relatively low number of nests, is considered important because of its location. Loggerheads are more flexible than other sea turtle species in their nesting site fidelity (Dodd 1988). Small nesting beaches between “major” nesting areas could contribute to the genetic homogeneity of the nesting populations. Koroni beach, located in the southern Peloponnese, between the large western nesting aggregations of loggerhead turtles in the Ionian Sea (*i.e.*, Zakynthos, Kyparissia Bay) and the eastern ones of Lakonikos Bay, may play such a role (see Carreras et al. 2007).

Koroni beach and the bordering marine area have been recently included in the EU's NATURA 2000 network of protected sites (code: GR2550010, name: “Marine area of southern Messinia SCI”) (Fig. 1), and a specific Management Agency has been appointed but not yet fully activated. It is expected that the



Fig. 7. Loggerhead nest in Koroni predated by canids tunneling under the protective metal grid. Bamboo sticks anchor the grid to avoid its displacement by predators (Photo: Smaro Touliaou/ ARCHELON).

continuation of the monitoring program will provide a strong basis for the conservation of this regionally important nesting population.

CONCLUSIONS

By analyzing long-term nesting data collected under a systematic monitoring program at the loggerhead sea turtle (*Caretta caretta*) nesting beach of Koroni, southern Peloponnese, Greece, we highlighted the existence of a small but important loggerhead population and its reproductive traits over time. Nesting success in the long-term is the highest recorded in Greece and annual nest numbers showed an upward trend in the most recent years. We also recorded significantly decreasing trends in clutch size, potentially reducing hatchling production in the long-term. We noted the significant decrease of incubation durations, caused apparently by increased temperatures due to global warming, and consequently a possible increase of female primary sex ratio. The high nest predation rates necessitate continuation of the current nest protection measures. The conservation status granted recently to the beach and to the adjacent marine area provides the backdrop for more specific protective measures in the future. This work demonstrates the value of maintaining a long-term program operated by an NGO, dedicated to studying and protecting sea turtles in Greece. We hope that ARCHELON will continue this systematic work, reveal major traits of reproductive parameters and hence assist in the management of this important loggerhead population.

Acknowledgments: Research permits were provided by the Ministry of Agriculture and the Ministry of Environment in Greece. We are grateful to field leaders and assistants, as well as to the many volunteers that worked in the area over the years. We also thank the local Municipality for their assistance. We appreciate constructive comments from two anonymous reviewers which greatly improved the quality of the manuscript.

Authors' contributions: DM planned the study, oversaw the continuation of program over the years and wrote the manuscript. GL archived the data and undertook the statistical analyses. AFR collected data, oversaw the program's methodology and assisted in writing the manuscript.

Competing interests: All authors declare that they have no conflict of interest.

Availability of data and materials: Not applicable.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

- Başkale E, Kaska Y. 2005. Sea turtle nest conservation techniques on southwestern beaches in Turkey. *Isr J Zool* **51**:13–26. doi:10.1560/G6NU-WG4N-07F5-PU6R.
- Bazigou F, Teneketzis K, Margaritoulis D, Kokkoris GD, Koutsoubas D. 2004. Contribution to the study of the nesting activity of the sea turtle *Caretta caretta* in the coasts of Koroni (SW Peloponnese, Ionian Sea) during the year 2003. *In: Proceedings of the conference of Hellenic Association of Ecologists and the Hellenic Zoological Society*. Gkiourdas Ekdotiki, Mytilene, Greece, pp. 173–181. (in Greek with abstract in English)
- Broderick AC, Godley BJ, Hays GC. 2001. Trophic status drives inter-annual variability in nesting numbers of marine turtles. *Proc Roy Soc B* **268**:1481–1487. doi:10.1098/rspb.2001.1695.
- Broderick AC, Glen F, Godley BJ, Hays GC. 2003. Variation in reproductive output of marine turtles. *J Exp Mar Biol Ecol* **288**:95–109. doi:10.1016/S0022-0981(03)00003-0.
- Carreras C, Pascual M, Cardona L, Aguilar A, Margaritoulis D, Rees A, Türkozan O, Levy Y, Gasith A, Aureggi M, Khalil M. 2007. The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. *Conserv Genet* **8**:761–775. doi:10.1007/s10592-006-9224-8.
- Casale P, Broderick AC, Camiñas JA, Cardona L, Carreras C, Demetropoulos A, Fuller WJ, Godley BJ, Hochscheid S, Kaska Y, Lazar B, Margaritoulis D, Panagopoulou A, Rees AF, Tomás J, Türkozan O. 2018. Mediterranean sea turtles: current knowledge and priorities for conservation and research. *Endang Species Res* **36**:229–267. doi:10.3354/esr00901.
- Casale P, Margaritoulis D (eds). 2010. *Sea turtles in the Mediterranean: Distribution, threats and conservation priorities*. IUCN, Gland, Switzerland.
- Dodd CK Jr. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). US Fish and Wildlife Service, Biological Report **88**(14).
- Elginöz E, Sönmez B, Ilgaz M, Altinkaya H. 2022. Local effort for the conservation of loggerhead sea turtles: Results of 2021 monitoring study on Çirali Beach. *Med Turt Bull* **1**:24–28.
- Hays GC, Taxonera A, Renom B, Fairweather K, Lopes A, Cozens J, Laloë J-O. 2022. Changes in mean body size in an expanding population of a threatened species. *Proc R Soc B* **289**:20220696. doi:10.1098/rspb.2022.0696.
- Laloë J-O, Cozens J, Renom B, Taxonera A, Hays GC. 2014. Effects of rising temperature on the viability of an important sea turtle rookery. *Nat Clim Change* **4**:513–518. doi:10.1038/NCLIMATE2236.
- Le Gouvello DZM, Girondot M, Bachoo S, Nel R. 2020. The good and bad news of long-term monitoring: an increase in abundance but decreased body size suggest reduced potential fitness in nesting turtles. *Mar Biol* **167**:112. doi:10.1007/s00227-020-03736-4.
- Margaritoulis D. 1988. Nesting of the loggerhead sea turtle *Caretta caretta* on the shores of Kyparissia Bay, Greece, in 1987. *Mésogée* **48**:59–65.
- Margaritoulis D. 2000. An estimation of the overall nesting activity of the loggerhead turtle in Greece. *In: Abreu-Grobois FA, Briseño-Dueñas R, Márquez-Millán R, Sarti-Martínez L (compilers)*

- Proceedings of the eighteenth international sea turtle symposium. NOAA Tech Memo NMFS-SEFSC-436, Miami, USA, pp. 48–50.
- Margaritoulis D, Argano R, Baran I, Bentivegna F, Bradai MN, Camiñas JA, Casale P, De Metrio G, Demetropoulos A, Gerosa G, Godley BJ, Haddoud DA, Houghton J, Laurent L, Lazar B. 2003. Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. *In*: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington DC, pp. 175–198.
- Margaritoulis D, Hiras G, Pappa C, Voutsinas S. 1996. Protecting loggerhead nests from foxes at the Bay of Kyparissia, western Greece. *In*: Keinath JA, Barnard DE, Musick JA, Bell BA (compilers) Proceedings of the fifteenth annual symposium on sea turtle biology and conservation. NOAA Tech Memo NMFS-SEFSC-387, Miami, USA, pp. 188–192.
- Margaritoulis D, Lourenço G, Riggall TE, Rees AF. 2022. Thirty-eight years of loggerhead turtle nesting in Laganas Bay, Zakynthos, Greece: A review. *Chelonian Conserv Biol* **21**(2):143–157. doi:10.2744/CCB-1531.1.
- Margaritoulis D, Rees AF. 2001. The Loggerhead Turtle, *Caretta caretta*, population nesting in Kyparissia Bay, Peloponnesus, Greece: Results of beach surveys over seventeen seasons and determination of the core nesting habitat. *Zool Middle East* **24**:75–90. doi:10.1080/09397140.2001.10637886.
- Margaritoulis D, Rees AF. 2003. Loggerhead nesting effort and conservation initiatives at the monitored beaches of Greece during 2002. *Mar Turtl Newsl* **102**:11–13.
- Margaritoulis D, Rees AF. 2006. Loggerhead nesting in Koroni, southern Peloponnesus, Greece: nesting data 1995–2002. *In*: Pilcher NJ (compiler) Proceedings of the twenty-third annual symposium on sea turtle biology and conservation. NOAA Tech Memo NMFS-SEFSC-536, Miami, USA, pp. 151–154.
- Mazaris AD, Schofield G, Gkazinou C, Almpnidou V, Hays GC. 2017. Global sea turtle conservation successes. *Sci Adv* **3**:e1600730. doi:10.1126/sciadv.1600730.
- Miller JD, Limpus CJ, Godfrey MH. 2003. Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. *In*: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington DC, pp. 125–143.
- Mortimer JA, Apoo J, Bratil B et al. 2022. Long-term changes in adult size of green turtles at Aldabra Atoll and implications for clutch size, sexual dimorphism and growth rates. *Mar Biol* **169**:123. doi:10.1007/s00227-022-04111-1.
- Mrosovsky N, Baptistotte C, Godfrey MH. 1999. Validation of incubation duration as an index of the sex ratio of hatchling sea turtles. *Can J Zool* **77**:831–835. doi:10.1139/Z99-039.
- Mrosovsky N, Kamel S, Rees AF, Margaritoulis D. 2002. Pivotal temperature for loggerhead turtles (*Caretta caretta*) from Kyparissia Bay, Greece. *Can J Zool* **80**:2118–2124. doi:10.1139/Z02-204.
- Mrosovsky N, Yntema CL. 1980. Temperature dependence of sexual differentiation in sea turtles: implications for conservation. *Biol Conserv* **18**:271–280. doi:10.1016/0006-3207(80)90003-8.
- Patel SH, Morreale SJ, Saba VS, Panagopoulou A, Margaritoulis D, Spotila JR. 2016. Climate impacts on sea turtle breeding phenology in Greece and associated foraging habitats in the wider Mediterranean region. *PLoS ONE* **11**:e0157170. doi:10.1371/journal.pone.0157170.
- Phillips KF, Stahelin GD, Chabot RM, Mansfield KL. 2021. Long-term trends in marine turtle size at maturity at an important Atlantic rookery. *Ecosphere* **12**:e03631. doi:10.1002/ecs2.3631.
- Pike DA. 2013. Climate influences the global distribution of sea turtle nesting. *Glob Ecol Biogeogr* **22**:555–566. doi:10.1111/geb.12025.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rees AF, Tzovani E, Margaritoulis D. 2002. Conservation activities for the protection of the Loggerhead Sea Turtle (*Caretta caretta*) in Kyparissia Bay, Greece during 2001. *Testudo* **5**(4):45–54.
- RStudio IDE. 2022. RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA. <http://www.rstudio.com/>.
- Schroeder BA, Foley AM, Bagley DA. 2003. Nesting patterns, reproductive migrations, and adult foraging areas of loggerhead turtles. *In*: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington DC, pp. 114–124.
- Sönmez B, Elginöz E, Ilgaz M, Altınkaya H. 2021. Nesting activity of loggerhead turtles (2013–2020) and 20 years abundance trend (2001–2020) on Çıralı Beach, Turkey. *Reg Stud Mar Sci* **44**:101758. doi:10.1016/j.risma.2021.101758.
- Teneketzis K, Margaritoulis D. 2019. Romanos beach, SW Peloponnese, Greece: increase of loggerhead sea turtle nests following a ten-year project (2009–2018). *In*: Tsikliras A, Dimarchopoulou D, Youlatos D (eds) Proceedings of the fourteenth international congress on the zoogeography and ecology of Greece and adjacent regions. Thessaloniki, Greece, p. 155.
- Tiwari M, Bjorndal KA. 2000. Variation in morphology and reproduction in loggerheads, *Caretta caretta*, nesting in the United States, Brazil, and Greece. *Herpetologica* **56**:343–356.
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM et al. 2010. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* **5**:e15465. doi:10.1371/journal.pone.0015465.
- Weishampel JF, Bagley DA, Ehrhart LM, Brian L, Rodenbeck BL. 2003. Spatiotemporal patterns of annual sea turtle nesting behaviors along an East Central Florida beach. *Biol Conserv* **110**:295–303. doi:10.1016/S0006-3207(02)00232-X.
- Willson A, Witherington B, Baldwin R, Tiwari M et al. 2020. Evaluating the long-term trend and management of a globally important loggerhead population nesting on Masirah Island, Sultanate of Oman. *Front Mar Sci* **7**:666. doi:10.3389/fmars.2020.00666.
- Yerli S, Canbolat AF, Brown LJ, Macdonald DW. 1997. Mesh grids protect loggerhead turtle *Caretta caretta* nests from red fox *Vulpes vulpes* predation. *Biol Conserv* **82**:109–111. doi:10.1016/S0006-3207(97)00003-7.
- Zbinden JA, Bearhop S, Bradshaw P, Gill B, Margaritoulis D, Newton J, Godley BJ. 2011. Migratory dichotomy and associated phenotypic variations in marine turtles revealed by satellite tracking and stable isotope analysis. *Mar Ecol Prog Ser* **421**:291–302. doi:10.3354/MEPS08871.