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Exponential Increase in a Loggerhead Sea Turtle Nesting Population: Investigating the Role of Multi-decadal Nest Protection in Kyparissia Bay, Greece

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Predation of nests by a multitude of terrestrial predators is a major threat to sea turtle populations worldwide. Destruction of eggs decreases hatching success and reduces hatchling recruitment. The 43.5-km beach of Kyparissia Bay in Greece, hosting a large nesting population of loggerhead sea turtles (*Caretta caretta*), is subject to heavy nest predation by canids. Over 50% of nests were annually depredated in the 1980s and this triggered in 1992 an intensive long-term nest protection program through which the predation rate was reduced to about 13%. Continuous beach monitoring over decades revealed that nest numbers started to increase after 17–20 years from the onset of nest protection and in recent years reached exponential dimensions. Similarly, yearly tagging of nesting turtles showed, in the last decade, a significant increase in the percentage of neophyte turtles, *i.e.*, those considered to be nesting for the first time. We attribute this extraordinary increase of nests largely to the maturing of hatchlings saved due to the intensive nest protection, since the time lag of 17–20 years falls within the boundaries of the maturation time of Mediterranean loggerheads. Our conclusion is further discussed in relation to the evolution of nest numbers at the nearby predator-free Zakynthos rookery that over the same time frame shows no significant increase of nests, although both populations share the same foraging habitats, and exhibit low nesting interchange, similar temperature regimes and female mortalities.

Key words: *Caretta caretta*, Conservation, Population trend, Predation, Monitoring

BACKGROUND

Sea turtles nest on land, on specific beaches, by excavating an egg chamber where they deposit a clutch of eggs which is incubated in the warm environment within the sand (Miller 1997). Non-human (or natural) predation of nests is a major threat worldwide to incubating sea turtle eggs; various animal groups such as invertebrates, crabs, reptiles, birds and mammals prey on sea turtle nests, with the most destructive egg predators by far being small to medium-sized mammals (see Stancyk 1995, for a review). High egg predation can have severe consequences on hatchling recruitment (Chaloupka and Limpus 2001; Türkozan et al. 2003; Engeman et al. 2012), which, after a number of years, may lead to population declines (Heithaus 2013). Conversely, natural predation of eggs and hatchlings provides food to a variety of animal populations in coastal ecosystems (Heithaus 2013). Anti-predator methods for sea turtle nest protection vary worldwide according to the specific problem created by the predators. Historically, these methods include relocation

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of nests to protected beach hatcheries, *in situ* fencing of nests, averting predators through chemicals, and control of predator populations (see Stancyk 1995, for a review).

Two species of sea turtles breed in the Mediterranean, the loggerhead sea turtle *Caretta caretta* and the green sea turtle *Chelonia mydas*. The majority of loggerhead nests are hosted in Greece, Turkey and Cyprus while most green turtle nests are found in Turkey, Cyprus and Syria, with fewer nests of both species laid in Israel, Lebanon and Egypt (Casale et al. 2018). Both species are affected by predation of their nests. Main predators are jackals, foxes, and feral or stray dogs, which visit the nesting beaches at night, dig into the nests, and consume eggs and hatchlings (Casale et al. 2018 and references therein). In the Mediterranean, the method of *in situ* fencing of nests is widely used as an effective nest protection measure (Yerli et al. 1997; Kornaraki et al. 2006). In Greece, where only the loggerhead turtle breeds regularly, some island nesting beaches (*i.e.*, Zakynthos, Crete) are devoid of jackals and foxes, and therefore nest predation there is negligible (Casale et al. 2018). In contrast, the nesting population at Kyparissia Bay, a major rookery in western Peloponnese, monitored by ARCHELON since 1984, was under severe pressure from high predation rates; about 50% in 1987 (Margaritoulis 1988). The first attempts to mitigate nest predation culminated in an intensive nest protection program from 1992 onwards.

Nest numbers from Kyparissia Bay have been published up to and including the 2002 nesting season (Margaritoulis and Rees 2001; Rees et al. 2002; Margaritoulis and Rees 2003). Nest numbers are used as a proxy for population size, and this metric is required for international agreements such as the European Union (EU)'s Marine Strategy Framework Directive (MSFD) and the reporting requirements of the Barcelona Convention.

Here, we provide the nest protection data for the period 1984–2021 and, by combining nest numbers of the period 2003–2024 with published data of the previous periods, we comment on the long-term trends of the nesting activity. Our main objective was to determine if intensive nest protection may contribute to higher numbers of nests after the increased annual cohort of hatchlings have matured and started breeding.

MATERIALS AND METHODS

Study site

Kyparissia Bay in western Peloponnese, Greece, is an open bay facing southwestwards in the Ionian Sea. Turtle nesting occurs along the 43.5-km beach length between the rivers Alfios and Arcadikos (from about 37.6124°N, 21.4536°E to about 37.2908°N, 21.6914°E; WGS 84) with nesting intensity increasing from north to the south (Margaritoulis and Rees 2001) (Fig. 1). The nesting beach has been divided, since 1984, into 12 Sectors (O, A–K) of uneven lengths (Fig. 1). Most of the coastal area is largely undeveloped with a wide beach platform backed by dunes and pine forests, with the exception of Sector O, located in front of the settlement Kalo Nero, featuring a narrow beach scattered with rocks in places and being increasingly developed with houses, hotels, and a coastal road. The southernmost four Sectors (O, A–C), concentrating most nesting in the bay, were characterized as the core nesting area (Margaritoulis and Rees 2001). The coastal terrestrial part of Kyparissia Bay, including the core nesting area and the adjacent marine area, until the 25-m isobath, are included in the NATURA 2000 network of protected sites under the EU's Habitats Directive (see Rees et al. 2023).

Field methods

The three Sectors A–C (totalling 7.3 km in length) have been closely monitored since 1984, with possible nests checked for eggs (by hand excavation until the top egg is uncovered) and, once verified, nests were monitored until hatching, as described in Margaritoulis and Rees (2001). Nest monitoring revealed a heavy loss of nests due to mammal predation, which led to taking the first pilot protection measures against this threat (Margaritoulis 1988). In 1994, the southernmost Sector O (2.2 km), previously being only occasionally visited, was included in the systematic monitoring work, and in 2013 Sector D (4.3 km) was also included (Fig. 1). Further, the northernmost Sectors E–K (totalling 29.7 km) were surveyed through weekly (or more frequent) surveys during four nesting seasons (2017–2019, and 2021).

From 1992 until 2021 all identified nests at the closely monitored sectors were protected, mainly *in situ*, through the use of a flat metal grid over the egg-chamber, anchored with bamboo sticks hammered around the edge (Fig. 2). A low percentage of nests, missed to be classified as such at the first survey after oviposition, were discovered later through hatchling emergence or predation events. Some nests were relocated (and protected) to higher locations on the beach to avoid inundation by seawater. Nests affected by photo pollution were shaded or "boxed" (*i.e.*, a wooden box placed above the nest retains hatchlings so that they can be collected and released on a dark stretch of beach) to mitigate against disorientation of hatchlings.

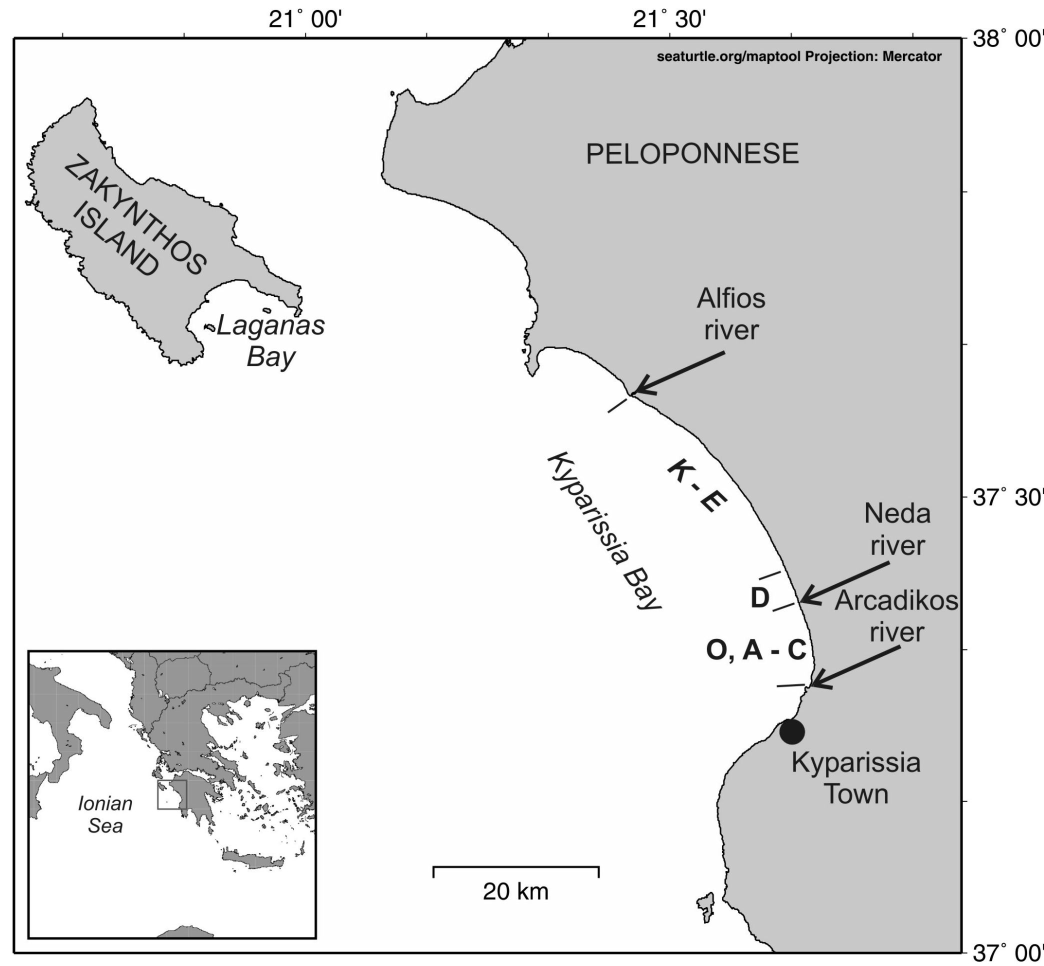

Fig. 1. Sketch map of Kyparissia Bay showing beach sectors between the rivers Alfios and Arcadikos. The core nesting area is contained in Sectors O and A–C, between the rivers Neda and Arcadikos. Laganas Bay in Zakynthos, a well-known loggerhead nesting area, starts at about 42 km, WNW from Alfios River.

Fig. 2. Predated sea turtle nest, despite protection through a metal grid anchored with bamboos. Increased humidity on beach sand permits foxes to tunnel below the grid and reach the eggs (Photo: ARCHELON).

All protected nests were monitored until hatching. In case of a nest predation, destroyed eggs were removed from the opened nest and the intact eggs were reburied and protected. After 2021, the intensity of protection measures was relaxed, by fencing about 70% of nests, because of the noted great increase of nests.

Tagging of nesting turtles was conducted since the beginning of the 1980s in parts of the monitored area, with varying intensity depending on human resources, as described by Margaritoulis et al. (2020). Turtles bearing old tags or scars attributed to lost tags were considered as "remigrants", while turtles with no tags or scars were conceived as "neophytes".

Statistical analyses

The Mann-Kendall trend test was used to identify monotonic trends in time series data and Spearman's Rank Correlation was used to test for a correlation between the percentage of predated nests and the percentage of protected nests. Tests were carried out in R version 4.3.3 (R Core Team 2024).

RESULTS

In the period 1984–1989, an average of 6.7% of laid nests were protected per year (annual range = 2.5–13.6%) (Fig. 3). In 1990 and 1991, 43.6% of laid nests were protected (annual range = 40.2–45.9%). Between 1992 onwards and 2021 included, an average of around 89.1% (annual range = 81.9–95.1%) of laid nests were protected at the currently monitored area (Fig. 3). The remaining nests that were not protected in the period 1992–2021 were nests that could not be located during the first survey after oviposition and were identified as such at a later stage, usually through predation or hatching. Predation rate was negatively correlated with protection rate. Spearman's Rank Correlation, rho = -0.606, $p < 0.001$ (Fig. 3).

Over the 41-year period (1984–2024), and along the three Sectors A-C (length: 7.3 km), we confirmed a total of 41,788 nests. The annual number of nests showed extreme annual fluctuations, ranging from 174 to 5,524 nests (median = 500 nests) (Table S1). Similarly, nesting density varied annually from 23.8 to 756.7 nests/km (median = 68.5 nests/km). Systematic monitoring of the southernmost Sector O (2.2 km) over the 31-year period (1994-2024) provided a median annual value of 176 nests (range = 92–1,225 nests) (Table S1). The annual nest density ranged from 41.8 to 556.8 nests/km (median = 80 nests/km). Monitoring work on Sector D (4.3 km), undertaken over 12 years, starting in 2013, provided a median annual number of 460 nests (range = 175–1,270 nests) (Table S1). The annual nest density on Sector D ranged from 40.7 to 295.3 nests/km (median = 107 nests/km). In total, all five southern Sectors (O, A–D), monitored consistently in the 12-year period (2013–2024), confirmed an average annual number of 3,535 nests (range = 1,461–

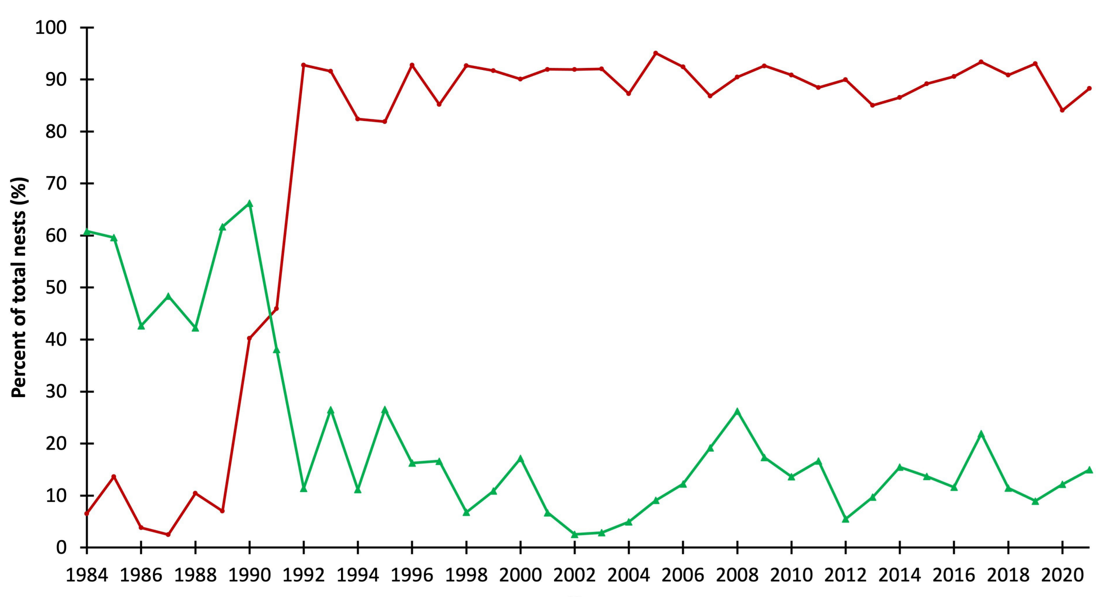

Fig. 3. Nest protection rate (red line) and nest predation rate (green line) in the period 1984–2021 in Kyparissia Bay. Data refer to Sectors A–C with the inclusion of data from Sector O since 1994, and of Sector D since 2013. Massive nest protection started in 1992. Protection measures after 2021 (not shown in the graph) were relaxed because of the noted large increase of nests.

8,019 nests) and an average nest density of 256.2 nests/km (range = 105.9–581.1 nests/km) (Table S1).

An exponential increase of nests was observed at the unfailingly monitored, for 41 years, Sectors A–C (Fig. 4). The data show a significant monotonic increase in nest numbers over time (Mann-Kendall trend test; $p < 0.0001$, tau = 0.707). The increase seems to start somewhere in the period 2008–2011. Large increases were noted in Sector O, consistently monitored in the 31-year period 1994–2024, as well as in Sector D, monitored for the 12-year period (2013–2024) (Fig. 4).

The spatial distribution of nests, confirmed during four years (2017–2019, and 2021) along all sectors (Table 1), provided the opportunity to estimate that the 8,019 nests counted in the record year 2024 in the southernmost five Sectors (O, A–D) (Table S1) indicate a total number of around 9,100 nests along the entire Kyparissia Bay (Fig. 5).

Multidecadal results of tagging provided an interesting temporal evolution of neophyte turtles over the years. Through the 1980s to 1992, the percentage of neophytes reduced from 100% to 50% as existing members of the population were tagged. This level stabilised at about 40% until 2002, when it bottomed out at just under 30% for two years. Subsequently the levels have increased, and since about 2009 to present, the percentage of neophytes has averaged around 60% (Fig. 6), but with a positive trend, providing evidence that an increased percentage of "new" turtles is entering the nesting population.

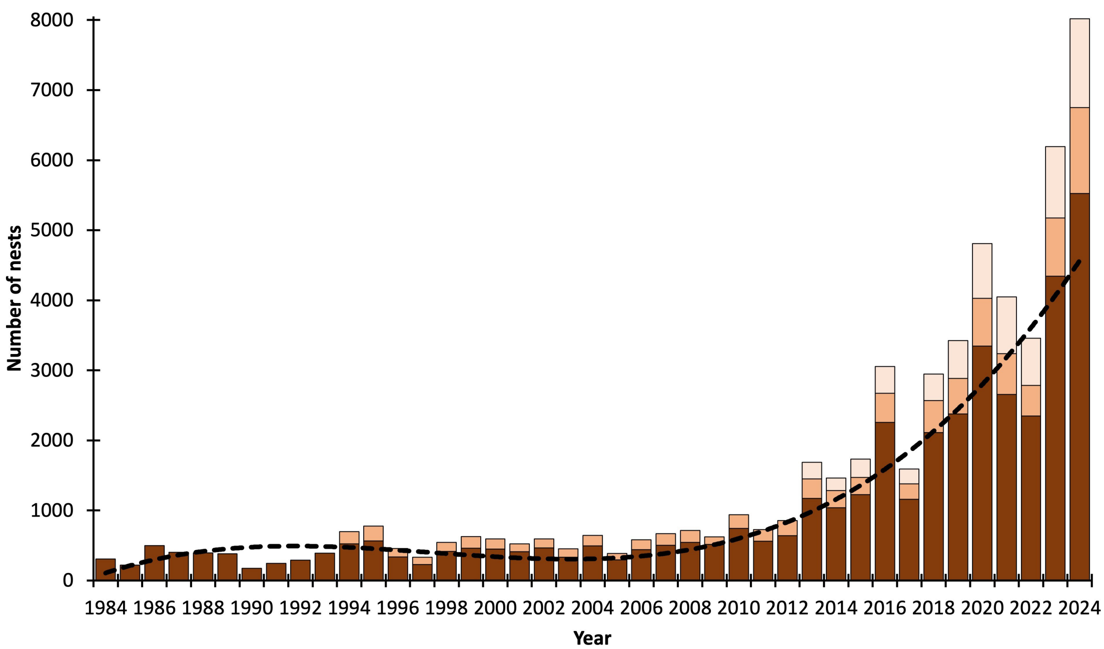

Fig. 4. Annual number of nests per Sectors A-C (dark brown) monitored unfailingly since 1984, Sector O (mid-brown) monitored since 1994, and Sector D (pale-brown) monitored since 2013. The polynomial trend line refers to Sectors A–C.

Table 1. Nest numbers, nesting contribution and nesting density per sector(s) during four years (2017–2019, and 2021) when all beach sectors were surveyed along the 43.5-km Kyparissia Bay

Sectors (from south towards north)	Year				Nesting contribution (%)	Mean nesting density (nests/km/year)
	2017	2018	2019	2021		
O (2.2 km)	219	456	509	583	13.0	200.8
A–C (7.3 km)	1159	2111	2376	2654	60.8	284.2
D (4.3 km)	213	380	540	813	14.3	113.1
E–K (29.7 km)	164	481	633	352	11.9	13.7
Overall (43.5 km)	1755	3428	4058	4402	100.0	78.4

DISCUSSION

We described the magnitude and the efficacy of nest protection measures, mainly against nest predation, in the monitored sectors of Kyparissia Bay. The year 1992 signals the start of systematic massive protection of nests, after which the annual predation rate fell to about 13%. The relatively large annual fluctuations of predation rates after 1992 are attributed to temporal changes of predator populations or their activity. Further, occasional rains—although not frequent in the area—and excess humidity assisted foxes to tunnel below the protective grids, as noted also in the loggerhead rookery of Koroni, southern Peloponnese (Margaritoulis et al. 2023).

The evolution of the annual nest numbers in the longest monitored Sectors A–C, over 41 years (1984–2024), showed an exponentially increasing trend. The large increase of nests documented in the southern sectors of Kyparissia Bay appeared also in the northern

Fig. 5. Partial view of the core nesting area of Kyparissia Bay showing the extremely high nest density towards the end of the nesting season in the record year (2024). Nests are distinguished by the bamboos that anchor the flat protective grids above the nests (Photo: D. Fytilis/ARCHELON).

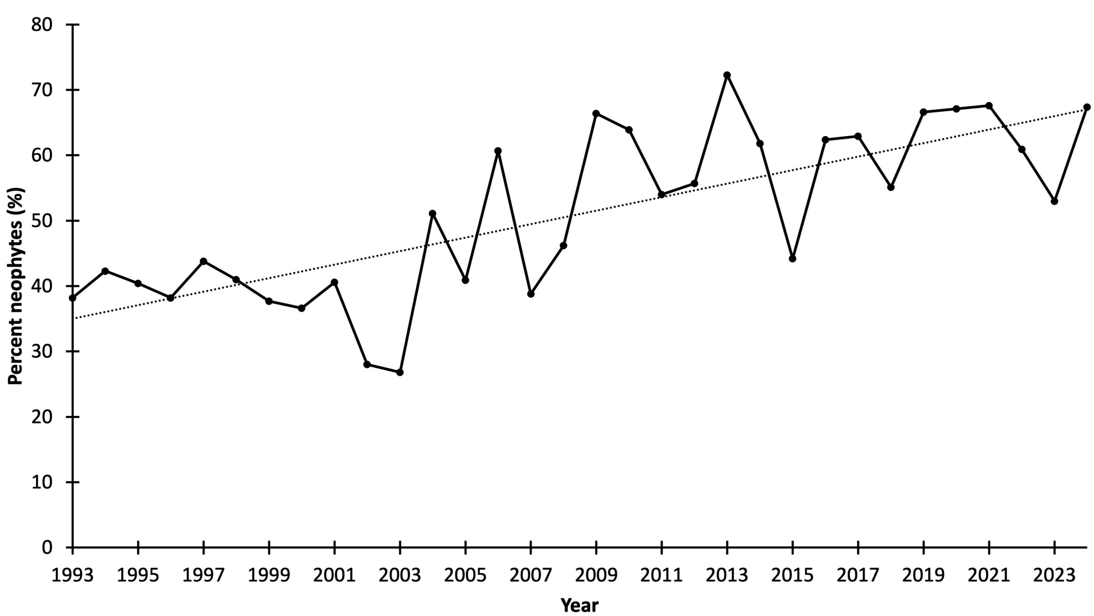

Fig. 6. Annual percentage of neophyte loggerhead turtles encountered during tagging work in Kyparissia Bay in the period 1993–2024. The data show a significant monotonic increase of neophyte percentage in the nesting population (Mann-Kendall trend test; $p < 0.0001$, tau = 0.535).

sectors. A comparison of nest numbers in Sectors E-K surveyed in the six-year period 1984–1989 (mean = 56.3 nests/year; Margaritoulis and Rees 2001) and in the recent four-year period (2017–2019, and 2021; mean = 407 nests/year), provides an overwhelming increase of 623%. The spatial distribution of nests along the entire Kyparissia Bay (43.5 km) in the recent period (2017–2019, and 2021) is similar to the spatial distribution documented during the surveys of the period 1984–1989 (Margaritoulis and Rees 2001), indicating the likely levels of precision incorporated in the phenomenon of natal homing.

The increase of nests in Kyparissia Bay seems to start somewhere in the period 2008–2011, which is about 17–20 years from the start of the aforementioned large-scale nest protection in 1992, and this time-lag falls within the limits of age at maturity, estimated by three aging methods, for loggerhead turtles in the Mediterranean (14.9–34.5 years; Casale et al. 2018). In a similar situation, from US Virgin Islands, the increase of the leatherback sea turtle (*Dermochelys coriacea*) nesting population was explained by an aggressive nest protection program initiated about 20 years ago, coinciding with the maturation age of leatherback turtles (Dutton et al. 2005). Conversely, Santos et al. (2000) and Hawkes et al. (2005) studying loggerhead nesting populations, respectively in Brazil and in Bald Head (USA), explained the non-increase of nests after 20 and 24 years of protection by the longer maturation time of loggerheads in the western Atlantic, meaning that more years would be needed to observe such an increase.

Nest numbers are considered reliable proxies of the number of adult females in a sea turtle population and, hence, of their conservation status. Consequently, a sustained large increase of nests is likely to reflect a real increase in the number of adult females. The assertion that the population nesting in Kyparissia Bay is increasing is supported by the increase of "neophyte" turtles that are encountered since about 2008, *i.e.*, after 17 years from the onset of massive protection of nests in 1992. Notwithstanding, some caution is needed here because the large increase of nesting turtles, under more or less similar over the seasons tagging effort, may bias the actual percentage of neophytes as proportionately fewer turtles are tagged each season.

In the last years there have been increases in sea turtle populations across the globe reflecting conservation efforts (Mazaris et al. 2017; Hays et al. 2025). In the Mediterranean, positive trends in nest counts of 16 index nesting sites were recorded in the latest IUCN Red List assessment for Mediterranean loggerheads (Casale 2015). Also Casale et al. (2018), comparing 21 nesting sites in the Mediterranean between two arbitrary periods (until 1999 and onwards from 2000), found an overall population increase of about 26%. This increase cannot be compared with the about four-fold (294%) increase at Kyparissia Bay (Sectors A–C), exhibited between the same periods, *i.e.*, 1984–1999 (mean = 365 nests/year) and 2000–2024 (mean = 1,438 nests/year), documented herein.

Our conclusion is further supported by comparing the temporal pattern of nests in Kyparissia Bay with those at Zakynthos over the 41-year period 1984–2024 (Fig. 7). Nest numbers in Kyparissia Bay (Sectors A–C) gradually reached, and since 2015 exceeded, those recorded at Zakynthos, once hosting the largest loggerhead nesting aggregation in the Mediterranean (Margaritoulis et al. 2003). Both nesting populations belong to the same genetic stock (Carreras et al. 2007; Carreras et al. 2014) and share the same foraging habitats, mainly in the Gulf of Gabés (north Africa) and in the Adriatic Sea, as documented by tag returns (Margaritoulis et al. 2003; Lazar et al. 2004), satellite tracking and stable isotope analyses of adult females (Zbinden et al. 2008; Schofield et al. 2013; Haywood et al. 2021; ARCHELON, unpub data). In addition, the striking similarity of the annual nesting fluctuations in both populations (see Fig. 7) provides additional evidence that the turtles nesting in Kyparissia Bay and in Zakynthos come from the same foraging areas, because nesting fluctuations depend largely on food availability influenced by environmental and oceanographic conditions at the foraging areas (Broderick et al. 2001; Solow et al. 2002). Nevertheless, despite the proximity of the two nesting habitats and the common foraging areas, Zakynthos nesting population has not shown any sizable increase and is considered stable in the long term, notwithstanding the operation of a conservation program since 1984 and an exceptional conservation status in the form of a National Marine Park since 1999 (Margaritoulis et al. 2022). An apparent explanation of this discrepancy is that the increased hatchling recruitment in Kyparissia Bay, due to the multidecadal elimination of predation, out-paced the more or less stable recruitment in the predation-free nesting areas of Zakynthos.

It is understood that a number of other factors, besides the elimination of predation, may have caused a population growth, such as (1) the increase of incubation temperatures (because of climate change) producing proportionately more female hatchlings and hence more nests (Laloë et al. 2014; Sousa-Guedes et al. 2025), (2) immigration of females from other nesting areas (Sato et al. 1997; Girard et al. 2021), (3) increased survivorship of adult females (Marco et al. 2012).

Existing data on hatchling feminization in Zakynthos and Kyparissia Bay do not show a sizeable difference in primary sex ratios. Female hatchling ratios were calculated for Kyparissia Bay to be about 70% (Rees and Margaritoulis 2004), and for Zakynthos to be 68–75% (during 2002–2003; Zbinden et al. 2007) and to 73.2–80.6% (during 2007–2009; Katselidis et al. 2012). Therefore, it does not seem plausible that the increase of nests in Kyparissia Bay can be attributed to a higher feminization of hatchlings in Kyparissia Bay in relation to those emerging in Zakynthos.

According to the ongoing long-term tagging projects conducted in both areas, no considerable drifting of nesters from Zakynthos to Kyparissia Bay has been detected. From a sample of 2,971 female turtles tagged in Zakynthos and Kyparissia Bay, over a 15-year period (1982–1996), only two turtles from Zakynthos were observed nesting in Kyparissia Bay and four turtles from Kyparissia Bay nested in Zakynthos (Margaritoulis 1998). A similar magnitude of nesting interchange, between the two areas, is demonstrated in more recent years (Rees et al. 2017; ARCHELON, unpub data). Further, Schofield et al. (2010) reported that although 10 out of 13 tracked females from Zakynthos made inter-nesting forays up to 100 km (some turtles approaching Kyparissia Bay), none of them nested at alternative sites. Other nearby nesting areas that could affect the size of the Kyparissia Bay population, through the immigration of nesting turtles, do not hold the necessary population level. For instance, the Romanos rookery, at the southwestern Peloponnese coast, south of Kyparissia Bay, showed an annual average of 18 nests and an increasing trend over the 10-year period 2009–2018 (Teneketzis and Margaritoulis 2019).

Could the large increase of nests at Kyparissia Bay be a result of lower mortality of adult females there in comparison to female deaths at Zakynthos? Both nesting populations suffer mortalities during the breeding season. From the archive of ARCHELON's stranding data, we obtained that in the 19-year period (2005–2023), 187 female turtles died in Zakynthos and 159 females in Kyparissia Bay. We believe that, although the two nesting populations were gradually becoming increasingly dissimilar, the overall difference in female mortality (28 turtles over 19 years) is rather trivial to justify the exponential growth of the Kyparissia Bay population against the long-term "stability" of the Zakynthos population.

Lastly, although favourable conditions at the shared foraging areas can increase in some specific years the nesting population, due to synchronization of nesting cohorts, in our case the almost continuous surge of nests in Kyparissia Bay reduces this possibility.

We therefore believe that the documented astonishing increase of nests in Kyparissia Bay was mostly caused by the long-term massive nest protection that started in 1992, *i.e.*, 17 years before the onset of the increase.

The presented nesting data, updating previous information, provide a basis to delineate better the core nesting area in Kyparissia Bay. Taking into account the nesting distribution during the recent years when

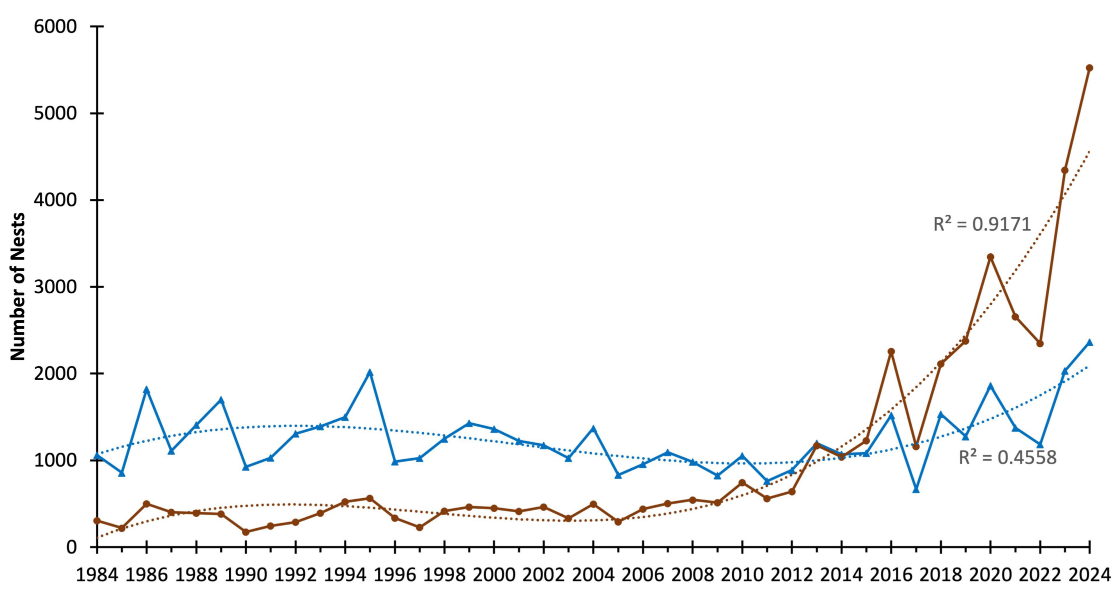

Fig. 7. Comparison of annual nest numbers and trends in Kyparissia Bay (Sectors A–C; brown lines) and in the nearby nesting area of Zakynthos (blue lines) for the 41-year period 1984–2024. Zakynthos data from Margaritoulis et al. (2022) and ARCHELON (2022 2023 2024). Trend lines are polynomials of third order.

the entire bay was surveyed (Table 1), we recommend that the core nesting area should expand northwards and include Sector D (4.3 km of beach length), which contributes 14.3% of all nests in the bay. Hence, the proposed core nesting area, comprised of the southernmost five Sectors (O, A–D), totaling 13.8 km in length, would host more than 88% of the total nesting effort across the entire Kyparissia Bay. This culminates in a nesting level of 3,535 nests/year and a nest density of 256.2 nests/km (both represent average values of the 12-year period 2013–2024). In the record year (2024), these five sectors hosted 8,019 nests, which were laid by about 2,350 individual turtles, considering a clutch frequency of 3.4 nests/year/female (Rees et al. 2023). Of note, these five sectors are all included in the EU's Natura 2000 site GR2550005 (Thines Kyparissias) (see Rees et al. 2023).

The herein presented extraordinary increase of nesting population at Kyparissia Bay certainly bears an impact on the current population assessments of the Mediterranean Management Unit (Wallace et al. 2023), as well as on national marine turtle population estimates employed under other schemes (*e.g.*, Favorable Reference Values in the EU's Natura 2000 network, MSFD).

Nevertheless, the lack of nesting data before 1984 and in view of the "shifting baseline syndrome" (Pauly 1995 in Bjorndal et al. (1999)), according to which scientists tend to describe population changes taking as a starting point the onset of their work, make us cautious in considering the noted increase as a "recovery" of the nesting population. It is unknown if there were more turtles nesting before the start of our work in 1984 or if natural agents, such as predation and inundation, kept numbers under balance. The continuing increase of nests in Kyparissia Bay raises directly the question: how many turtles are necessary for a viable population in the long term? It is not easy to answer this question as several factors are missing, such as survival rates at sea and population dynamics traits. In Greece, there are nesting beaches with thriving nesting populations, albeit small, with tens of nests, like those in Romanos (Teneketzis and Margaritoulis 2019) and Koroni (Margaritoulis et al. 2023). Further, the deprivation of a food source from the local fox population may have a consequence in the dynamics of the local terrestrial ecosystem (Heithaus 2013). Therefore, additional studies are needed to understand the interaction between sea turtle nesting and predators, and also to conceive the impact of an increased sea turtle population on marine and coastal ecosystems.

In the meantime, conservation efforts in Kyparissia Bay should continue because loggerheads in the Mediterranean face many threats that reduce their survival probabilities; especially those nesting in Greek rookeries appear as mostly affected by anthropogenic mortalities at sea (Casale et al. 2014).

CONCLUSIONS

A long-term massive nest protection program at the loggerhead sea turtle rookery of Kyparissia Bay, Greece, decreased nest predation rates from about 50% to 13%. Systematic nest counts revealed an exponential increase of nests after 17–20 years from the onset of the intense nest protection scheme in 1992. This time-lag falls within the limits of the maturation time of loggerhead turtles in the Mediterranean. Furthermore, there has been a proportional increase of neophyte turtles during the same period. Additionally, the nesting population at the nearby Zakynthos rookery, devoid of nest predations, does not show such an increase although both populations share the same foraging habitats. Considering these lines of evidence, we conclude that the dramatic increase in the number of nests at Kyparissia Bay is largely attributable to increased hatchling recruitment, resulting from the large-scale nest protection program, and the saved hatchlings' return after maturation to nest on their natal beaches.

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Authors' contributions: DM planned the study, oversaw the continuation of the program over the years, and wrote the manuscript. AFR collected data, made the figures, and assisted in writing the manuscript. TER oversaw the program's methodology, and collected and archived data. All authors approved the final version of the manuscript.

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Ethics approval consent to participate: Not applicable.

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Supplementary materials

Table S1. Nest numbers per monitored beach sector(s) in southern Kyparissia Bay during the 41-year period 1984–2024 (x: not monitored). (download)