Herpetological Conservation and Biology 18(3):551–559.
Submitted: 28 February 2023; Accepted: 16 October 2023; Published: 16 December 2023.

Internesting Habitat Preference and Updated Clutch Frequency Values for Loggerhead Turtles (*Caretta caretta*) Nesting in Kyparissia Bay, Greece

ALan F. Rees[1], Nancy Papathanasopoulou, Panagiotis Papoulias, Galini Samlidou, Panagiota Theodorou, and Dimitris Margaritoulis

ARCHELON, the Sea Turtle Protection Society of Greece, Solomou 57, GR-104 32 Athens, Greece
[1]Corresponding author, email: alanfrees@gmail.com

Abstract.—**Adult female Loggerhead Turtles (*Caretta caretta*) migrate from foraging to breeding areas to lay multiple clutches over 1–2 mo. As sea turtles may travel long distances between nests, efforts are needed to determine their at-sea movements and habitat preferences within breeding areas. In turn, the predictable presence of turtles in these habitats can facilitate the use of straightforward management measures. We used satellite telemetry, novel GSM telemetry, and drone surveys to determine the distribution of turtles at-sea during the breeding period at the largest nesting site for Loggerhead Turtles in the Mediterranean - Kyparissia Bay, Greece. We found that turtles largely remain within the 50 m isobath and close to where they nest, although specific sites (i.e., protected waters of a nearby harbor) farther away from the nesting beach were also used. We also combined our satellite telemetry data with previous data to update the estimated mean clutch frequency (the number of clutches laid by turtles during a single breeding period) for this population. The new estimated mean clutch frequency ranged from 3.3–3.5, which were slightly lower than the previous estimate (3.8) for the same breeding population even though they remain higher than values published for other locations in the Mediterranean. Our findings confirm that conservation measures can be adequately defined within spatially local and temporally restricted boundaries and that population sizes based on clutch frequencies lower than 3.3 are likely to be overestimated in Kyparissia Bay.**

Key Words.—drone; Mediterranean Sea; population estimation; sea turtle; telemetry

Introduction

Upon reaching sexual maturity, Loggerhead Turtles (*Caretta caretta*) return to breed at natal areas at predictable times of the year. In the Mediterranean, the Loggerhead Turtle breeding season runs from late May or early June to August and most nesting occurs in the eastern basin (Casale et al. 2018). Individuals deposit 1–5 clutches on sandy beaches at approximately two-week intervals (Omeyer et al. 2019; Rees et al. 2020), meaning a single female may remain in breeding habitats for up to about 2 mo. Internesting period of turtles is defined as the time between laying the first and last clutches of the season. The predictable presence of turtles in an area for 2 mo suggests relatively simple management and conservation measures can be implemented in internesting habitats to protect large numbers of the biologically valuable adult turtles. Immediately after laying the final clutch of the season, turtles depart the area (Dujon et al. 2017) for over-wintering/foraging areas that may be hundreds of kilometers away (Margaritoulis et al. 2003; Zbinden et al. 2008; Schofield et al. 2013; Patel et al. 2015; Snape et al. 2016).

The use of satellite telemetry and GPS loggers means that internesting habitats are well established for the important Greek Loggerhead Turtle nesting area at Laganas Bay on Zakynthos Island, Greece (Zbinden et al. 2007; Schofield et al. 2007, 2010). In addition, drones have been used over large-scale areas to determine the whereabouts of turtles during the summer breeding period in western Greece, which includes Zakynthos (Dickson et al. 2021). Kyparissia Bay (starting from about 30 km southeast of Zakynthos) includes a 44 km sandy beach, extending from the Alfios River in the north to the Arcadikos River, just past Kalo Nero village in the south (Fig. 1). In recent years, it has hosted the largest aggregation of nesting Loggerhead Turtles in the Mediterranean (Casale et al. 2018), with most nesting occurring in the southern core area of 9.5 km, from the river Neda, next to the village of Elaia, southwards (Margaritoulis and Rees 2001).

The conservation program in the area, carried out by ARCHELON (www.archelon.gr), focuses on land-based activities of nest protection and public awareness. The core nesting habitat and surrounding area, including the beach to the north, are designated Natura 2000 protected sites (GR2550005 and GR2330005, respectively; Fig. 1). The nearshore marine habitats of Kyparissia Bay, stretching to the 25 m isobath, are also designated as a Natura 2000 site (GR2330008; Fig. 1). A Presidential Decree (PD; Government Gazettes D 391/03-10-2018, D 414/12-10-2018) stipulated

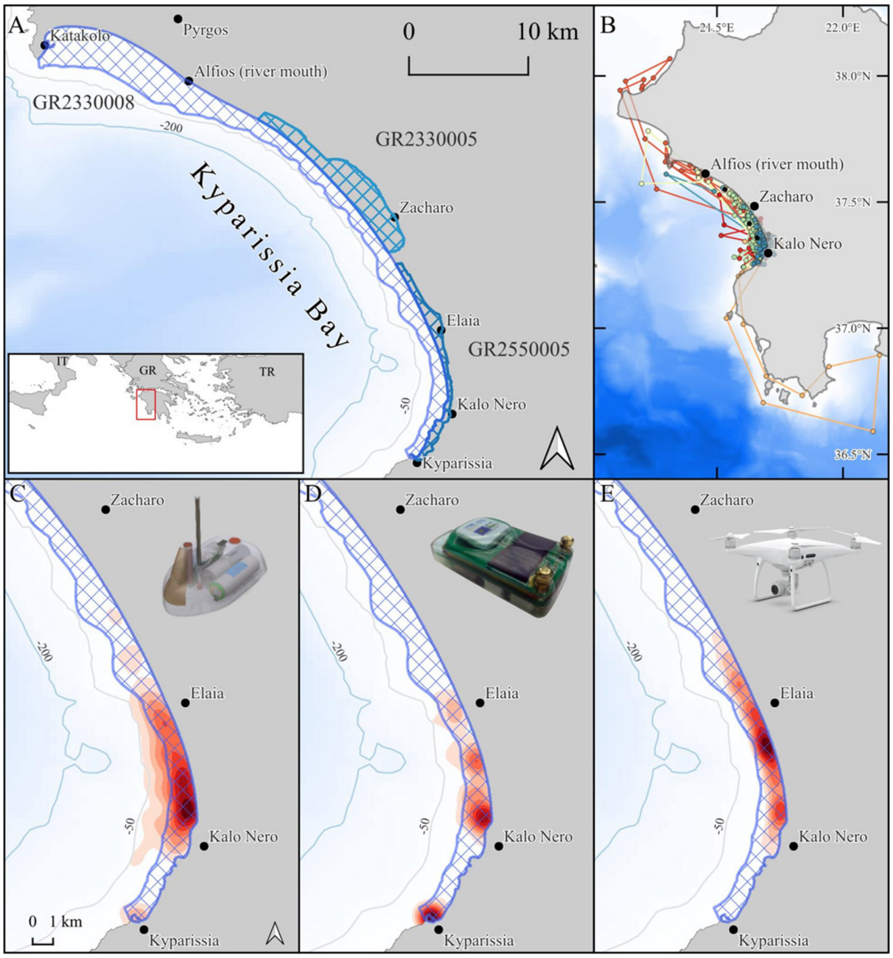

Figure 1. Locations, routes, and hotspots during the internesting period for Loggerhead Turtles (*Caretta caretta*) in Kyparissia Bay, Greece. (A) Kyparissia Bay showing the Natura 2000 sites relating to sea turtles in blue hatching. GR2330008: Thalassia Periochi Kolpou Kyparissias (Marine Area Kyparissia Bay), GR2330005: Thines Kai Paraliako Dasos Zacharos, Limni Kaiafa, Strofylia, Kakovatos, and GR2550005: Thines Kyparissias (Neochori - Kyparissia). Inset map depicts the map extent for panel B. (B) Filtered locations for 30 nesting turtles tracked with Argos satellite transmitters from southern Kyparissia Bay between 2005 and 2022, showing movement out of the Bay for three individuals. (C) Location Heatmap for the same turtles in panel B. (D) Location heatmap for 14 nesting turtles tracked with novel GSM-GPS transmitters from southern Kyparissia Bay between 2019 and 2021. (E) Location heatmap for 505 turtle observations during nearshore drone surveys of Kyparissia Bay, undertaken in June and July 2020. These surveys covered the area offshore of the nesting beach and not Kyparissia harbor. Heatmaps present distribution density with darker reds representing higher kernel densities. Isobaths are derived from global GEBCO bathymetry dataset (www.gebco.net/). Country abbreviations are GR = Greece, IT = Italy, TR = Türkiye.

the protection of the integrity of the designated area, including protected species occurring there, like the Loggerhead Turtle. The PD provides some protective measures for nesting sea turtles, including speed limits for sea craft within one nautical mile (1.852 km) of the coast and prohibition of nighttime sport fishing. Both regulations are in place during the summer breeding period; however, additional measures at sea may be implemented through a Management Plan, which is legally required for the area.

Potential conservation and management plans should be based on scientific data to be most effective, least obtrusive, and sufficiently robust to counter any lobbying against the proposed measures. Intrinsic to the protection of turtles in their internesting habitat is the requirement to know where the turtles are, if they are evenly distributed throughout the region, and how far from shore they venture. Recently, drone research has provided some indications of the whereabouts and movements of turtles in the nearshore habitats of southern Kyparissia Bay during the summer (Dickson et al. 2022).

To build on the previous work, we used drones to determine the locations of turtles during the breeding season (June and July) along the entire nesting habitat and not only the core area covered by Dickson et al (2022). Additionally, we used telemetry, which facilitated obtaining turtle locations farther offshore, despite this being potentially biased due to sampling site selection and the nest site fidelity of turtles (repeatedly returning to the same area of beach to nest). We also used breeding period residency data from a subset of the current telemetry study, together with data published in Rees et al. (2020), to re-examine the average number of clutches laid by Loggerhead Turtles during a single breeding period.

Materials and Methods

We located turtles for the telemetry studies along the 9.5 km core nesting area at the south of Kyparissia Bay (37.3399°N, 21.6952°E) and undertook drone surveys that covered the entirety of the Kyparissia nesting area (Fig. 1). For the telemetry study, we patrolled between 2300 and 0300 to locate nesting turtles. We selected turtles for study upon completion of a nesting emergence, confirmed by observation of oviposition. We attached satellite transmitters (2005: Model A-1010; Telonics Inc. Mesa, Arizona, USA, and 2018-2022: Model SPOT-375; Wildlife Computers, Redmond, Washington, USA) and GSM transmitters (Global Systems for Mobile communications; novel GPS location transmitters designed and built under the EU funded LIFEeuroturtles project; www.euroturtles.eu) to a subset of flipper-tagged Loggerheads to track them using the Argos system (www.argos-system.org) and the GSM cellular phone network, respectively. We deployed 30 satellite transmitters and 20 GSM transmitters at different points along the nesting beach. We moved turtles into large plastic boxes to retain them on the beach during transmitter deployment (about 2 h). We attached the transmitter to the carapace of the turtle, centered over the second vertebral scute, using the Wildlife Computers attachment kit (or equivalent) and their recommended methods (www.wildlifecomputers.com).

For the drone study, we used a DJI Phantom 4 Pro quadcopter (www.dji.com) that recorded 4k video (4096 × 2160 pixels) with GPS location (updated at 1 sec intervals) embedded in the video. We used the Litchi application (www.flylitchi.com) to design a flight plan of three 2-km parallel transects, which could be flown using a single battery. The transects were positioned at about 150, 300, and 450 m from the shore (Fig. 2). We flew at 40 m altitude with the camera at nadir, which gave a visual strip width of approximately 100 m and ensured any turtles were large enough to be conspicuous within all video frames (Fig. 2). Surveys were flown at 35 km/h. We replicated this flight plan 20 times to cover the entire length of the Kyparissia Bay nesting habitat. We conducted drone surveys, covering all 20 flight plans, twice; once per month in June and July 2020. We additionally flew the drone manually over Kyparissia harbor in June 2021 to verify the indications from telemetry that the area was occupied by breeding turtles. When flying over the harbor, we recorded turtle presence using 4K video in a non-systematic manner, flying the drone at different heights and following varying trajectories.

Data processing.—For the satellite tags, we used the Wildlife Computers data portal (www.wildlifecomputers.com) to retrieve and archive Argos location data. We used the first best location per day from Argos Location Classes 3, 2, 1 (Class 3 assumed better than Class 2, better than Class 1; www.argos-system.org) to register turtle positions and movement, with expected accuracy of no better than 250 m. We retained inland locations to avoid skewing average position data offshore. For the GSM transmitters with expected accuracy < 100 m, we subsampled location data to retain the first location per transmitter per day, hence providing data at intervals comparable to the satellite tags.

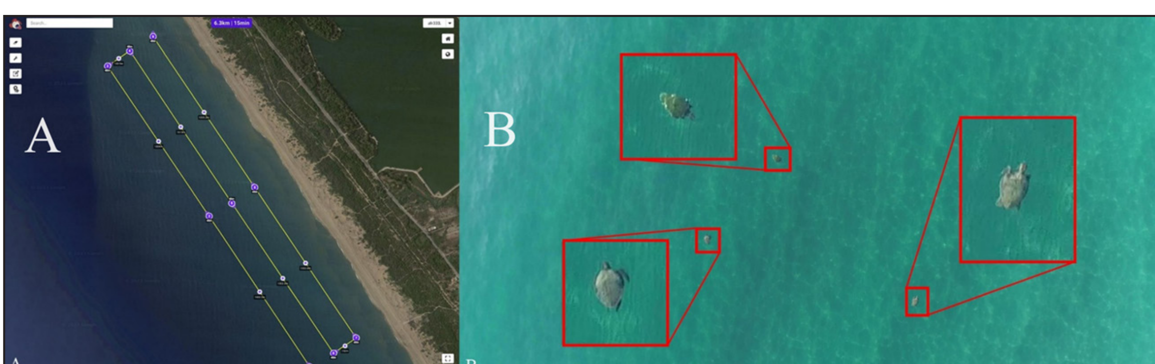

Figure 2. Use of drones to collect presence data of Loggerhead Turtles (*Caretta caretta*) in Kyparissia Bay, Greece. (A) Example survey route flown by drone, comprising three parallel 2-km transects at about 150 m, 300 m, and 450 m from shore. Twenty of these routes were distributed to cover the entire length of the nesting beach. (B) Example frame from the 4K drone footage with Loggerhead Turtles highlighted.

For the whole-bay drone surveys, we combined turtle sightings from both surveys to create a single dataset of turtle presence. No attempt to determine detection probably was undertaken, so we considered all turtle counts observed minimums. We processed extracts from the video recorded over Kyparissia harbor using the Image Composite Editor v2 software (www.microsoft.com) and stitched together extracts into a composite image covering the majority of the harbor. We counted the number of turtles present in this composite image and calculated the minimum density of animals present using the area of the harbor (0.105808 km^2) derived from a polygon drawn in Google Earth Pro (Google LLC, Mountain View, California, USA). We mapped data in QGIS (v3.28; www.qgis.org). We determined turtle high-use areas by using the integrated Heatmap (Kernel Density Estimation) symbology function (https://docs.qgis.org/3.28/en/docs/user_manual/processing_algs/qgis/interpolation.html#heatmap-kernel-density-estimation) with 1,000 m at scale entered as the radius and automatic selected for Maximum Value. Kernel Density Estimates (KDE) are affected by unequal numbers of locations from different individuals; nevertheless, the use of only one location per turtle per day and a narrow range in the number of locations suggest the KDEs were not unduly affected.

Determination of clutch frequency.—We estimated clutch frequency using data from turtles tracked from the same area in 2019 (n = 12; published in Rees et al. 2020) and from 2022 (n = 8; this study), which were assumed to be tracked from their first nest of the season, as they received transmitters within the first two weeks of the nesting season. We determined the total number of days the turtles were present in the internesting habitat (internesting period), assuming time of deployment as day 0 and that turtles depart the nesting area the day after they deposit their last clutch (Dujon et al. 2017). We divided this total by potential internesting intervals (from clutch deposition to next clutch deposition) restricted to a minimum 13 d and maximum 20 d (Margaritoulis 1983) to generate a likely minimum and maximum number of clutches per turtle. We assessed interannual differences for estimated minimum and maximum clutch frequencies using the Mann-Whitney-Wilcoxon Test with significance at $\alpha = 0.05$.

Results

Satellite telemetry.—We deployed the first satellite transmitter on 6 June 2005. We deployed a further nine between 13 and 19 June 2018, which was sufficiently late in the nesting season for the turtles to have previously nested and we did not use these in determination of average clutch frequency (see Rees et al. 2020 for discussion). We deployed 12 more transmitters between 7 and 12 June 2019 and eight between 8 and 13 June 2022 (Table 1), which was the start of the respective nesting seasons, when we assumed turtles have not previously nested within that year.

Table 1. Minimum (Min) and maximum (Max) number of clutches and internesting interval, nest to nest, between 13 and 20 d (in parentheses) deposited by Loggerhead Turtles (*Caretta caretta*) tracked in Kyparissia Bay, Greece, from the start of the nesting season derived from duration of the internesting period of turtles. An asterisk (*) indicates turtle data from Rees et al. (2020). Turtle Departure is the date the turtle commenced seasonal migration away from the nesting area.

Turtle	Tag Deployment	Turtle Departure	Internesting Period (days)	Min #Clutches	Max #Clutches
2019-1*	7 June 2019	15 July 2019	38	3 (19.0)	3 (19.0)
2019-2*	8 June 2019	7 July 2019	29	3 (14.5)	3 (14.5)
2019-3*	8 June 2019	29 July 2019	51	4 (17.0)	4 (17.0)
2019-4*	9 June 2019	16 July 2019	37	3 (18.5)	3 (18.5)
2019-5*	9 June 2019	20 July 2019	41	4 (13.7)	4 (13.7)
2019-6*	9 June 2019	19 July 2019	40	3 (20.0)	4 (13.3)
2019-7*	10 June 2019	11 July 2019	31	3 (15.5)	3 (15.5)
2019-8*	11 June 2019	11 July 2019	30	3 (15.0)	3 (15.0)
2019-9*	12 June 2019	21 July 2019	39	3 (19.5)	4 (13.0)
2019-10*	10 June 2019	28 July 2019	48	4 (16.0)	4 (16.0)
2019-11*	11 June 2019	10 July 2019	29	3 (14.5)	3 (14.5)
2019-12*	12 June 2019	12 August 2019	61	5 (15.3)	5 (15.3)
2022-1	8 June 2022	6 July 2022	28	3 (14.0)	3 (14.0)
2022-2	8 June 2022	9 July 2022	31	3 (15.5)	3 (15.5)
2022-3	8 June 2022	16 July 2022	38	3 (19.0)	3 (19.0)
2022-4	10 June 2022	28 July 2022	48	4 (16.0)	4 (16.0)
2022-5	11 June 2022	9 July 2022	28	3 (14.0)	3 (14.0)
2022-6	12 June 2022	15 July 2022	33	3 (16.5)	3 (16.5)
2022-7	12 June 2022	12 July 2022	30	3 (15.0)	3 (15.0)
2022-8	13 June 2022	22 July 2022	39	3 (19.5)	4 (13.0)

After data filtering, we retained 905 daily locations. Excluding data from the 2005 turtle that provided only intermittent locations (n = 5 d with locations), we retained an average of 31.0 locations (loc) per turtle (± 11.9 [standard deviation] loc, range from 10–59 loc, n = 29). Three turtles carried out looping movements that took them out of Kyparissia Bay even though they returned to the bay to nest; two turtles moved north, and one moved south (Fig. 1). The other 26 turtles remained within Kyparissia Bay, nearshore in shallow water generally < 50 m deep (Fig. 1). The main cluster of locations ranged over a distance of about 10 km from Kalo Nero in the south to just past Elaia in the north. A distinct hotspot of locations, representing seven turtles (23% of total, including the turtle from 2005), was present south of the nesting beach, centered on Kyparissia harbor (Fig. 1). We explored this specific location using a drone (see Drone Surveys). All location hotspots occurred within the marine Natura 2000 site designated in Kyparissia Bay.

GSM telemetry.—We deployed seven transmitters in 2019, three in 2020, and 10 in 2021 at different times within the nesting seasons. We obtained 174 d of location data from 14 of the 20 GSM devices (mean retained locations = 12.4 ± 9.8 loc; range from 1–27 loc). The other six devices failed and provided no location data. All locations were in the Kyparissia Bay area (Fig. 1). Highest densities of locations were in similar areas to those from satellite tracking, i.e., nearshore between Kalo Nero and Elaia, and a distinct hotspot of locations centered around Kyparissia harbor resulting from the presence of four turtles (29% of total). Again, all location hotspots occurred within the marine Natura 2000 site designated in Kyparissia Bay.

Drone surveys.—We recorded 505 turtle sightings from drone surveys along the entire nesting beach in Kyparissia Bay (Fig. 1); 320 were recorded in June and 185 in July. Similar to the results from the telemetry study, the highest density of turtles was at the southern part of the main nesting area, from Kalo Nero in the south and extending north past the limit of the previously defined core nesting area of Elaia. We recorded at least 100 turtles within the harbor from a single observation in late June 2021, which extrapolates to an observed minimum density of about 1,000 turtles/km^2 (Fig. 3). We did not try to determine the sex of turtles from the

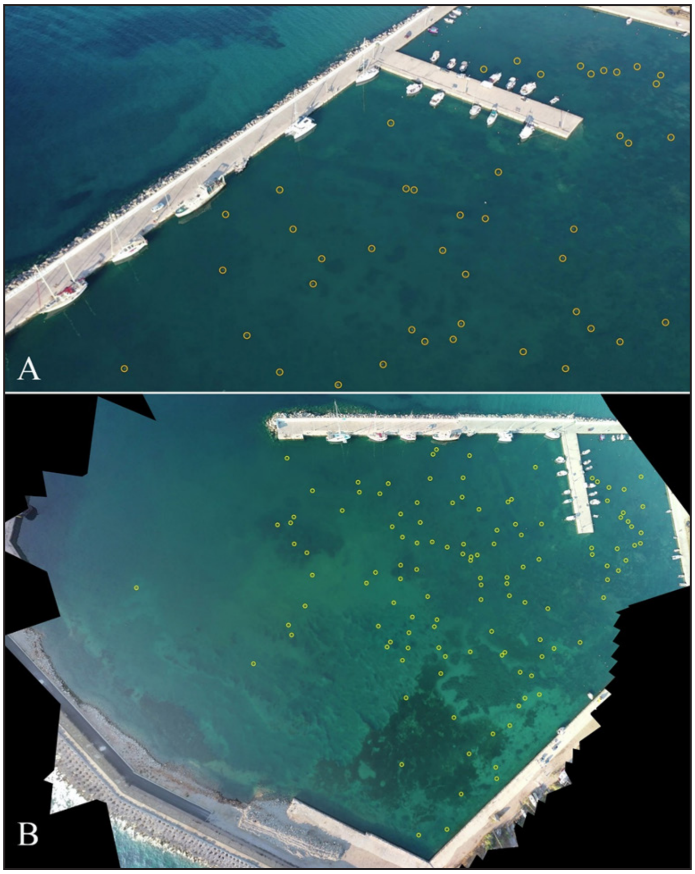

Figure 3. Drone survey imagery from Kyparissia harbor, Greece, in June 2021. (A) Single video frame showing 45 Loggerhead Turtles (*Caretta caretta*) present in one section of the harbor. (B) Composite image showing the high number and density of adult turtles congregating in the harbor (about 1,000 turtles/km^2). Yellow circles indicate the position of a turtle.

Table 2. Mean, standard deviation, range (minimum and maximum values), and sample size (n) of clutch frequency estimates per year restricted to internesting intervals, nest to nest, between 13 and 20 d of Loggerhead Turtle (*Caretta caretta*) from Kyparissia Bay, Greece.

	Maximum				Minimum			
Year	Mean	Standard Deviation	Range	n	Mean	Standard Deviation	Range	n
2019	3.6	0.7	3–5	12	3.4	0.7	3–5	12
2022	3.3	0.5	3–4	8	3.1	0.4	3–4	8

drone videos in the harbor; however, we expected male turtles to have departed the breeding area prior to the survey and we assumed that all observed turtles were adult females.

***Revised clutch frequency*.**—Only three turtles, with internesting periods of either 39 or 40 d, provided potentially different maximum and minimum clutch frequencies within the 13–20 d internesting interval time constraint (Table 1) as they could represent 3 or 4 clutches. All other internesting periods produced a single possible clutch frequency when constrained within the 13–20 d internesting interval range. The estimated maximum clutch frequency did not differ significantly between years ($W = 61.0$, $P = 0.263$; Table 2) giving a pooled, average clutch frequency value for 20 turtles of 3.5 ± 0.6 nests (range from 3–5 nests). Likewise, the estimated minimum clutch frequency did not differ significantly between years ($W = 58.5$, $P = 0.307$; Table 2) giving a pooled minimum clutch frequency for 20 turtles of 3.3 ± 0.6 nests (range from 3–5 nests) per turtle.

Discussion

***Distribution: in-water vs nesting*.**—The greater distribution of turtles towards the south of the bay from unbiased, but limited to 450 m from shore, drone surveys is in line with other drone surveys results from the area (Dickson et al. 2021) and reflects nesting density on adjacent beaches with most turtles present in the south (Margaritoulis and Rees 2001). This suggests that most turtles remain in waters nearby and somewhat perpendicular offshore from where they nest, but with some variation likely driven by prevailing winds (Dickson et al. 2022). It is therefore not surprising that turtles tracked after nesting on the southern section of beach showed residency to hotspots nearby. Similarly, Loggerhead Turtles tracked from Cyprus (Snape et al. 2018) and Zakynthos (Schofield et al. 2007) were shown to predominantly remain within a few kilometers of their nesting location suggesting this is a common trait for Loggerhead Turtles in the Mediterranean. Nevertheless, we also observed a key exception as the highest density of turtles was identified within Kyparissia harbor. This suggests that conditions within the harbor (shallow, calm, warm waters) were sufficiently better, supporting beneficial behaviors and egg maturation (see below), than offshore of the nesting area.

***In-water distribution: resident or itinerant*.**—Tracking data showed that Loggerhead Turtles nesting in Kyparissia Bay were found mainly occupying shallow nearshore habitats during their interesting period. This is similar to nesting turtles at other locations in Greece such as Laganas Bay, Zakynthos (Zbinden et al. 2007; Schofield et al. 2007, 2010) and Rethymno, Crete (Panagopoulou 2015), and elsewhere in the Mediterranean including southwest Turkey (Cerritelli et al. 2022) and Alagadi, Cyprus (Snape et al. 2018). This contrasts with Loggerheads from the northwest (NW) Indian Ocean, however, where four of 10 tracked turtles performed large-scale oceanic loops, up to 300 km away from the nesting area (Rees et al. 2010). Remaining nearshore in shallow waters likely enables turtles to conserve energy during their breeding season when they are generally considered not to be feeding (Bonnet et al. 2016). The shallow waters are warmed more than deeper offshore waters, meaning that egg maturation between clutches, which is temperature dependent (Sato et al. 1998; Hays et al. 2002), can proceed more quickly during the limited Mediterranean breeding period. The larger-scale movements out of Kyparissia Bay, made by three of the turtles during their breeding period, may reflect reduced breeding site fidelity. In these instances, the turtles all returned to Kyparissia Bay within an 11-d period, precluding the possibility of nesting elsewhere, so the precise purpose and drivers of these movements requires further study.

Tracking corroborated the drone surveys by showing that Kyparissia harbor was heavily used (20–30% of tracked individuals), however the precise number of turtles in the Kyparissia harbor hotspot cannot be determined, as some of the turtles were moving during the video recording process, and they may be represented more than once in the resulting composite image. Nevertheless, using data showing that nest numbers at Kyparissia Bay are close to 1,400, with an estimated clutch frequency of 3.3 to 3.5 per turtle per season, it appears that one roughly a quarter of all nesting turtles were present in the harbor during the survey. How the turtles learned about the location, by individual chance encounter, social facilitation (where naïve turtles follow more experienced individuals), or environmental cues, remains unknown and a fundamental knowledge gap in our understanding of marine turtle behavioral ecology. Fortunately, Kyparissia harbor features relatively low amounts of boat traffic and is used by only few artisanal fishers and no speedboats. Consequently, there is currently relatively little anthropogenic disturbance relative to what might exist at a commercial fishing harbor, which is an important consideration for conservation as boat strikes are a well-reported threat to turtles in Greece (Casale et al. 2018).

Revised clutch frequency and implications for population size.—Our conservative, revised estimated average clutch frequency of 3.3 to 3.5 clutches per turtle is similar to but lower than previously reported (3.8 clutches; Rees et al. 2020). These values could have been affected if we had started tracking turtles after their second or later nest of the season (as we assumed was the case for the turtles tracked in 2018) and would mean that the clutch frequencies we determined would be underestimations. Based on start dates of the nesting seasons obtained through intensive monitoring of the core nesting area (ARCHELON, unpubl. data), however, we are confident that this would be highly improbable for our included datasets. Nevertheless, the clutch frequency value in the current study remains above the values for Loggerhead Turtles from Cyprus, which at a population level is about two clutches per turtle but is shown to be about 1.5 clutches for first time nesters and nearer to three clutches for re-migrant turtles (Omeyer et al. 2021). The sample of turtles in Greece is likely to be a combination of first time and re-migrant turtles, but of unknown proportions, and hence we cannot determine how that might affect our clutch frequency results. Furthermore, our estimated clutch frequency is based on turtles nesting at the start of the breeding period, and intra-seasonal variation may lead to changes if later turtles lay more or fewer clutches. Despite relatively small yearly sample sizes, our results suggest that clutch frequency remains stable between seasons, with small levels of interannual variation for early-start nesters. We conclude that for Loggerhead Turtles nesting in Greece, estimates of the annual number of nesting turtles, based on the number of nests, should be calculated using a value of at least 3.3 clutches/female.

Conservation implications.—Our results show that the marine Natura 2000 site in Kyparissia Bay covers a large portion of the key summer habitat used by internesting turtles. Extending the seaward boundary to the 50 m isobath (ca. 1 km), however, would incorporate the majority of internesting turtle locations and the protection measures established therein would further benefit turtles. Given such a well-defined coastal zone of high occupancy during the breeding period, it will be relatively simple to design more structured conservation actions and mandates in future considerations of area zonation.

Kyparissia harbor has been revealed as a potentially important summer habitat for internesting turtles and boat collisions are only a potential problem to turtles because the harbor is currently lightly used and there have been no reports of boat strikes (ARCHELON, unpubl. data). The situation, however, requires ongoing monitoring to confirm continued use of the harbor by large numbers of turtles during the summer and any potential changes to the type and quantity of boat traffic using the harbor. If boat traffic increases, more defined measures specific to the harbor area can be introduced to reduce the potential impacts. Turtle nesting in Kyparissia Bay seems secure, with species and habitats currently protected by law, but improvements can be made in terms of more concrete conservation management plans and improved marine habitat delimitation based on our current extensive dataset.

Acknowledgments.—Drone surveys and GSM telemetry actions were funded under the European Union (EU) LIFEeuroturtles project. Satellite tracking was funded in 2005 by EU Life Nature Project Reduction of Mortality of *Caretta caretta* in the Greek Seas, and in 2018–2022 by the MAVA Foundation under the Conservation of Marine Turtles in the Mediterranean Region project (supervised by the Specially Protected Areas Regional Activity Centre of the United Nations Environment Programme). We thank Sammy Ball, Giannis Chalkias, Amy Feakes, Sicily Fiennes, Nathan Gibrat, Sevi Kapota, Eirini Kasimati, Anna Lamaj, Polymnia Nestoridou, Harriet Parsons, Odysseas Paxinos, Eve Pilmore, Kira Schirrmacher, Michalis Souroulidis and Dominic Tilley for assistance deploying the satellite tags. Research was carried out under permits No 96281/946/2 March 2004, 149645/3352/7 March 2017 and No 177335/2495/5 February 2019, No 118125/3261/21 January 2021 and 110967/3631/13 December 2021 to ARCHELON from the Ministry of Environment. The authors thank three reviewers and the handling editor for their input that directly improved the overall quality of the manuscript.

Literature Cited

Bonnet, X., D. Bradshaw, and R. Shine. 2016. Capital versus income breeding: an ectothermic perspective. Oikos 83:333–342.

Casale, P., A.C. Broderick, J.A. Camiñas, L. Cardona, C. Carreras, A. Demetropoulos, W.J. Fuller, B.J. Godley, S. Hochscheid, Y. Kaska, et al. 2018. Mediterranean sea turtles: current knowledge and priorities for conservation and research. Endangered

Species Research 36:229–267.

Cerritelli, G., P. Casale, D. Sozbilen, S. Hochscheid, P. Luschi, and Y. Kaska. 2022. Multidirectional migrations from a major nesting area in Turkey support the widespread distribution of foraging sites for Loggerhead Turtles in the Mediterranean. Marine Ecology Progress Series 683:169–177.

Dickson, L.C.D., K.A. Katselidis, C. Eizaguirre, and G. Schofield. 2021. Incorporating geographic scale and multiple environmental factors to delineate the breeding distribution of sea turtles. Drones 5:142. https://doi.org/10.3390/drones5040142.

Dickson, L.C.D., H. Tugwell, K.A. Katselidis, and G. Schofield. 2022. Aerial drones reveal the dynamic structuring of sea turtle breeding aggregations and minimum survey effort required to capture climatic and sex-specific effects. Frontiers in Marine Science 9:864694. https://doi.org/10.3389/fmars.2022.864694.

Dujon, A.M., G. Schofield, R.E. Lester, N. Esteban, and G.C. Hays. 2017. Fastloc-GPS reveals daytime departure and arrival during long-distance migration and the use of different resting strategies in sea turtles. Marine Biology 164:187. https://doi.org/10.1007/s00227-017-3216-8.

Hays, G.C., A.C. Broderick, F. Glen, B.J. Godley, J.D.R. Houghton, and J.D. Metcalfe. 2002. Water temperature and internesting intervals for Loggerhead (*Caretta caretta*) and Green (*Chelonia mydas*) sea turtles. Journal of Thermal Biology 27:429–432.

Margaritoulis, D. 1983. The inter-nesting interval of Zakynthos Loggerheads. Pp. 135–144 *In* Adaptations to Terrestrial Environments. Margaris, N.S., M. Arianoutsou-Faraggitaki, R.J. Reiter (Eds.). Plenum Press, New York, New York, USA.

Margaritoulis, D., and A.F. Rees. 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. Zoology in the Middle East 24:71–95.

Margaritoulis, D., R. Argano, I. Baran, F. Bentivegna, M.N. Bradai, J.A. Camiñas, P. Casale, G. De Metrio, A. Demetropoulos, G. Gerosa, et al. 2003. Loggerhead Turtles in the Mediterranean Sea: present knowledge and conservation perspectives. Pp. 175–198 *In* Loggerhead Sea Turtles. Bolten, A.B., and B.E. Witherington (Eds.). Smithsonian Institution Press, Washington, D.C., USA.

Omeyer, L.C.M., W.J. Fuller, B.J. Godley, R.T.E. Snape, and A.C. Broderick. 2019. The effect of biologging systems on reproduction, growth and survival of adult sea turtles. Movement Ecology 7:2. https://doi.org/10.1186/s40462-018-0145-1.

Omeyer, L.C.M., K.L. Stokes, D. Beton, B.A. Çiçek, S. Davey, W.J. Fuller, B.J. Godley, R.B. Sherley, R.T.E. Snape, and A.C. Broderick. 2021. Investigating differences in population recovery rates of two sympatrically nesting sea turtle species. Animal Conservation 24:832–846.

Panagopoulou, A. 2015. Sea turtles and small-scale fisheries: designing conservation policies for a marine area on Crete, Greece. Ph.D. Dissertation, Drexel University, Philadelphia, Pennsylvania, USA. 220 p.

Patel S.H., S.J. Morreale, A. Panagopoulou, H. Bailey, N.J. Robinson, F.V. Paladino, D. Margaritoulis, and J.R. Spotila. 2015. Changepoint analysis: a new approach for revealing animal movements and behaviors from satellite telemetry data. Ecosphere 6(12):1–13. https://doi.org/10.1890/ES15-00358.1.

Rees, A.F., S. Al Saady, A.C. Broderick, M.S. Coyne, N. Papathanasopoulou, and B.J. Godley. 2010. Behavioural polymorphism in one of the world's largest populations of Loggerhead Sea Turtles *Caretta caretta*. Marine Ecology Progress Series 418:201–212.

Rees, A.F., P. Theodorou, and D. Margaritoulis. 2020. Clutch frequency for Loggerhead Turtles (*Caretta caretta*) nesting in Kyparissia Bay, Greece. Herpetological Conservation and Biology 15:131–138.

Sato, K., Y. Matsuzawa, H. Tanaka, T. Bando, S. Minamikawa, W. Sakamoto, and Y. Naito. 1998. Internesting intervals for Loggerhead Turtles, *Caretta caretta*, and Green Turtles, *Chelonia mydas*, are affected by temperature. Canadian Journal of Zoology 76:1651–1662.

Schofield, G., A. Dimadi, S. Fossette, K.A. Katselidis, D. Koutsoubas, M.K.S. Lilley, A. Luckman, J.D. Pantis, A.D. Karagouni, and G.C. Hays. 2013. Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. Diversity and Distributions 19:834–844.

Schofield, G., C.M. Bishop, G. MacLean, P. Brown, M. Baker, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, and G.C. Hays. 2007. Novel GPS tracking of sea turtles as a tool for conservation management. Journal of Experimental Marine Biology and Ecology 347:58–68.

Schofield, G., V.J. Hobson, M.K.S. Lilley, K.A. Katselidis, C.M. Bishop, P. Brown, and G.C. Hays. 2010. Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. Biological Conservation 143:722–730.

Snape, R.T.E., A.C. Broderick, B.A. Çiçek, W.A. Fuller, F. Glen, K. Stokes, and B.J. Godley. 2016. Shelf life: neritic habitat use of a turtle population highly threatened by fisheries. Diversity and Distributions 22:797–807.

Snape, R.T.E., P.J. Bradshaw, A.C. Broderick, W.A. Fuller, K.L. Stokes, and B.J. Godley. 2018. Off-the-shelf GPS technology to inform marine protected areas for marine turtles. Biological Conservation 227:301–309.

Zbinden, J.A., A. Aebischer, D. Margaritoulis, and R. Arlettaz. 2007. Insights into the management of sea turtle internesting area through satellite telemetry. Biological Conservation 137:157–162.

Zbinden, J.A., A. Aebischer, D. Margaritoulis, and R. Arlettaz 2008. Important areas at sea for adult Loggerhead Sea Turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. Marine Biology 153:899–906.

ALan F. Rees began his career in sea turtle research and conservation in 1994 with ARCHELON in Greece, after he had gained an M.Sc. in Biotechnology from the University of the West of England, UK. He earned his Ph.D. in 2013 from the University of Exeter, UK. In 2022 he established the MedTurtle Bulletin; a newsletter dedicated to the sea turtles of the Mediterranean. ALan is a Regional Vice Co-chair of the Marine Turtle Specialist Group of the Species Survival Commission of the International Union for Conservation of Nature. He is currently an independent sea turtle researcher. (Photographed by Panos Dendrinos).

Nancy Papathanasopoulou is an environmental law and management expert, and a Lawyer at Athens Bar Association. She studied in Greece and in France, and has worked on sea turtle conservation and research for more than 30 y in several capacities (volunteer, student, lawyer, legal consultant, team member, project coordinator, project manager, drone pilot/researcher), and in several countries. Nancy has also worked as a consultant on international environmental issues with the Deputy Minister for Environment in Greece (2000–2003), the Secretary General for Environment in Oman (2008–2011), and the Emir of Kuwait (2010–2016). (Photographed by Panagiotis Papoulias).

Panagiotis Papoulias has a Ph.D. in Theoretical and Computational Physics. He is the founder of Science Seals LLC, a company formed around his personal areas of interests and expertise. His current focus is developing a drone for remote observation of environmental habitats and working as a drone pilot for environmental projects. In physics, Panagiotis is investigating the mechanisms fields localize to produce particles, as well as developing the theory behind a spectroscopic method based on precursors. His past work also involved development of mobile applications for environmentalists and conservationists. (Photographed by Nancy Papathanasopoulou).

Galini Samlidou has a Conservation Biology degree (University of Plymouth, UK) with 10 y of experience in sea turtle conservation. She has managed some of the largest Mediterranean sea turtle projects run by ARCHELON (Peloponnese, Crete, Zakynthos, Amvrakikos Gulf; 2019–2023) while also coordinating fieldwork for Life Euroturtles. Galini has run fundraising and public awareness programs, involving stakeholders and highlighting the ecological and socio-economic value of conserving wildlife. She is currently with the Angling Trust UK coordinating the Catchwise project and continues contributing to initiatives addressing tourist-related impacts on sea turtles through public engagement. (Photographed by Kostas Papafitsoros).

Panagiota Theodorou is a Lawyer and has served ARCHELON for the last 11 y in various positions. She has strong background in environmental legislation, in shaping and implementing environmental policy, in managing multiethnic teams, in organizing and implementing projects. Panagiota has significant experience in co-operation, putting pressure, but also in lobbying with authorities, in managing various stakeholders towards sustainable development. She has represented ARCHELON in various committees, conferences and workshops and has practiced law in Athens and Chalkis Bar Associations, while she has studied law in Greece and Germany. (Photographed by Hugo Baron).

Dimitris Margaritoulis is a founding member (1983) of ARCHELON, the Sea Turtle Protection Society of Greece, which through its pioneer field projects became a model non-governmental organization. Dimitris took part in the elaboration of the Global Strategy for the Conservation of Marine Turtles of Marine Turtle Specialist Group (MTSG) of the International Union for Conservation of Nature and served for a 10-y period (1999–2009) as the Mediterranean Regional Chair for MTSG. He received several awards, among them the Athens Academy Award (1984) and the Life Achievement Award of the International Sea Turtle Society (2010). (Photographed by Anna Kremezi-Margaritoulis).