Zoological Studies **64:**61 (2025)

Dispersal and Foraging Strategies of Adult Loggerhead Sea Turtles (*Caretta caretta*) Breeding in Kyparissia Bay, Greece: Implications for Conservation

ALan F. Rees[1,*], Tasos Dimalexis[2], George Mikoniatis[3], and Yannis Vavassis[3]

[1]*Turtles from Above, 48 Beaumont Road, Plymouth, PL4 9BW, UK. *Correspondence: E-mail: alanfrees@gmail.com (Rees). Tel: +44 (0)7758-406-250*

[2]*Nature Conservation Consultants (NCC) Ltd, 20 Pentelis Avenue, GR 152 35 Vrilissia Athens, Greece. E-mail: adimalexis@n2c.gr (Dimalexis)*

[3]*HELLENiQ UPSTREAM S.A., HELLENiQ ENERGY Holdings S.A, 8A Chimarras Street., GR 151 25 Maroussi Athens, Greece. E-mails: gmikoniatis@upstream.helleniq.gr (Mikoniatis), yvavassis@upstream.helleniq.gr (Vavassis)*

(Received 28 July 2025 / Accepted 13 October 2025 / Published -- 2025)
Communicated by Tzu-Gao Lin

Sea turtles are long-lived wide-ranging animals undertaking long-distance breeding migrations showing fidelity to both foraging and breeding sites. This fidelity has led to population structuring with regional management units defined for globally distributed species. Loggerhead sea turtles (*Caretta caretta*) have established such a management unit in the Mediterranean, with the greatest number of turtles breeding in Greece. Kyparissia Bay, Greece, has been identified as the location with largest nesting aggregation of loggerhead turtles in the Mediterranean. Determining where this aggregation of turtle migrates to outside the breeding season is important for its continued conservation. Long-distance flipper tag recaptures have identified certain high use areas for these turtles but lack route data and certainty that recaptured turtles are resident in the area of capture. Satellite tracking has been used to validate such tag return data and generate insights into turtle migrations patterns and their relationship with phenological and fecundity metrics. Here we recorded turtles' curved carapace lengths as a metric for general body size and deployed Argos satellite transmitters on 11 adult loggerhead sea turtles (8 females, 3 males) during their breeding period in Kyparissia Bay, to examine the implications of their selected migratory routes and foraging strategies. Average carapace length (±SD) was 82.0 cm (±4.6 cm) for the 8 female turtles and 86.0 cm (±5.5 cm) for the 3 males. Turtles were tracked for an average of 326.9 days. End points for the tracked turtles were grouped into four distinct regions The Aegean Sea was the end point for 3 turtles, and the Adriatic Sea was the end point for another 3 turtles with one turtle spending an extended period in the northern Ionian. The northern Ionian Sea was the end point for a further 3 turtles and the Tunisian plateau was the end point for final 2 turtles. Six turtles migrated to restricted area foraging sites, 1 turtle remained nomadic for the entirety of its tracking duration, 2 turtles were semi-nomadic incorporating both restricted area foraging and large-scale movements during their tracking period, and the tracks of the final 2 turtles ceased before their behaviour type could be determined, but sedentary behaviour type was inferred. Notably the one turtle that remained nomadic was 6 cm shorter than the next shortest turtles, suggesting carry-over effects of the nomadic life-history. The turtles generally moved to locations that had been identified by flipper tag recaptures, however the tracking identified routes taken to get there, which were often highly convoluted. These foraging sites, also identified through other tracking studies of loggerhead turtles nesting elsewhere in Greece and from Cyprus, were often sites of high fishing activity and cause for concern for turtles present there. Given that up to around 2,000 turtles may nest in Kyparissia Bay during a single summer, we conclude that a larger number of turtles, over multiple years, should be tracked to obtain a more robust assessment of post-breeding migrations, foraging strategy adoption and their carry-over effects, which can then be used to better inform conservation and management actions.

Keywords: Marine turtle migration, Foraging sites, Tracking male sea turtles, Fisheries threats, Mediterranean Sea

Citation: Rees AF, Dimalexis T, Mikoniatis G, Vavassis Y. 2025. Dispersal and foraging strategies of adult loggerhead sea turtles (*Caretta caretta*) breeding in Kyparissia Bay, Greece: implications for conservation. Zool Stud **64:**61.

BACKGROUND

Sea turtles long lived slow to mature creatures inhabiting wide expanses of marine habitats over their lifetime (Musick and Limpus 1997). As adults they perform regular breeding migrations from foraging sites to breeding sites showing strong fidelity over successive reproductive periods (Broderick et al. 2007; Schofield et al. 2010; Shimada et al. 2019). These foraging sites host mixed stocks of turtles, which means that individuals from different rookeries congregate in the same foraging areas (Bowen and Karl 2007). Through these characteristics of natal homing (the propensity for sea turtles to return to breed on beaches they were themselves hatched) and site fidelity (where sea turtles nest in the same vicinity for each breeding season) global sea turtle metapopulations can be divided into regional management units (RMUs, Wallace et al. 2023) each with their own conservation status and needs (Wallace et al. 2025). Larger turtles from the onset of sexual maturity are considered to have higher reproductive value than smaller, younger turtles (Wallace et al. 2008). Consequently, determining the whereabouts of these biologically important adult turtles means targeted conservation and management measures can be set, which are likely to have disproportionate conservation benefit on threatened populations.

Flipper tagging capture-mark-recapture programmes on nesting beaches have existed for decades and are a somewhat effective way of determining the distribution of turtles away from their breeding sites (*e.g.*, Mortimer and Carr 1987; Limpus et al. 1992; Margaritoulis et al. 2007). However, tag returns only give point locations of turtle observations and single observations and do not give indication if a turtle is resident at the capture site or migrating through. They also depend on the turtles being observed and may therefore show bias in observation distributions. However, at least in the Mediterranean, distribution of nesting turtles tracked using satellite tags has been shown to support long-distance tag recapture data (Zbinden et al. 2008; Baldi et al. 2023).

Since the 1990s, satellite telemetry of sea turtles has become increasingly common (Godley et al. 2008; Hays et al. 2016) and complements tag return data through identifying migration routes and foraging locations of turtles after nesting (*e.g.*, Schofield et al. 2013a; Pilcher et al. 2014; Whittock et al. 2016). Tracking durations for individuals are such that sometimes even two-year remigrations back to the original nesting areas can be followed (*e.g.*, Rees et al. 2010; Schofield et al. 2010; Mingozzi et al 2016), providing remarkable insights into individual turtles' spatial movements, albeit at low sample sizes.

Attempts have been made to upscale tracking results to more population level sample sizes using differential stable isotope signatures of turtle tissues (generally for Carbon and Nitrogen) to define broadscale spatially explicit foraging locations. The benefit of stable isotope analyses (SIA) being the cost per individual to gather the relevant data is far less than for telemetry. This technique has proven moderately effective for certain turtle species in certain global locations (*e.g.*, Bradshaw et al. 2017; Ceriani et al. 2012) but not always so (Coffee et al. 2020).

Two species of sea turtle nest in the Mediterranean, the loggerhead turtle (*Caretta caretta*) and the green turtle (*Chelonia mydas*) and have both established their own endemic RMUs (Wallace et al. 2023). The loggerhead is the most numerous species and most commonly nests in Greece, Turkey, Cyprus and Libya (Casale et al. 2018). In Greece, the two most important nesting areas are Laganas Bay, Zakynthos Island and Kyparissia Bay, on the west coast of the Peloponnese (Casale et al. 2018). Flipper tag recaptures from both nesting areas revealed the most common foraging areas for turtles nesting at these locations are the Adriatic Sea and the Tunisian Shelf (Margaritoulis et al. 2007) and satellite tracking over 70 turtles from the Laganas Bay nesting site confirmed these findings for both adult female and male turtles (Zbinden et al. 2008; Schofield et al. 2013a).

Kyparissia Bay, which has recently overtaken Laganas Bay to host annually the most loggerhead nests in the Mediterranean region (Margaritoulis et al. 2025), has relatively less information published on migrations of the turtles breeding there. In addition to the reported flipper tag returns of Margaritoulis et al. (2007), Haywood et al. (2021) provide generalised foraging locations for 20 nesting females tracked after nesting there. The authors attempted to use SIA to determine similar scale foraging locations for a further 80 sampled turtles, however lack of isotopically distinct foraging regions for the population meant that untracked females could not be assigned to putative foraging grounds (Haywood et al. 2021).

In this study we aimed to identify migratory routes and foraging strategies for both adult male and female loggerhead turtles breeding in Kyparissia Bay. We also sought to determine other biologically relevant observations based on the behaviours of the tracked individuals with the goal of highlighting the conservation implications of their selected behaviours in the context of heterogenous regional fishing pressure.

MATERIALS AND METHODS

Transmitters

We used Wildlife Computers' (Wildlife Computers, Redmond, WA, USA) SPOT-375 Argos-linked satellite tags (https://www.argos-system.org/) to track female loggerhead turtles and Wildlife Computers' SPLASH10-385 to track male loggerheads on their post-breeding migrations. The tags were programmed with a 15 s transmission repetition rate, with no duty cycling but transmissions were limited to 250 day^{-1}. The Argos system provides locations classified to have different levels of accuracy, depending on the number of transmissions received during the satellite pass, and other factors (CLS 2016).

Turtles

We deployed satellite tags on 3 nesting turtles in 2021, 5 nesting females in 2022 and 3 breeding males in 2023. Nesting turtles were located at random on the southern core nesting area of the Kyparissia Bay nesting site (Margaritoulis et al. 2025). Full transmitter deployment methods have been previously described (Rees et al. 2023), in short, turtles were moved into a large plastic container after they had finished laying a clutch of eggs and completed the covering stage of their nesting behaviour. The carapace was cleaned and transmitter attached with epoxy and fibreglass sheets using the Wildlife Computers attachment kit (or equivalent) following the company's methods (wildlifecomputers.com).

Male turtles were captured at sea using the turtle rodeo technique (Ehrhart and Ogren 1999) in Kyparissia harbour, a location previously identified as hosting high densities of turtles during the breeding period (Rees et al. 2023 2025). To ensure these turtles were adult males in breeding condition we randomly targeted males that were mounted upon- or attempting to mount other turtles. Captured turtles were taken ashore and retained in a plastic container and we attached transmitters to them using the same methods as for nesting females.

We recorded the turtles' curved carapace lengths, notch to tip (CCL; see Bolten 1999) and the male turtles' tail lengths measured from the inner part of the notch between the supracaudal scutes to the tip of the outstretched tail. Both types of measurement were recorded to the nearest 0.5 cm. After measuring and transmitter attachment the turtles were released at the location they were obtained, generally within two hours of capture.

Data processing and presentation

Argos location data were automatically downloaded and archived in the Wildlife Computers' data portal (my.wildlifecomputers.com) for the lifespan of the tags. The data were pre-cleaned prior to state space modelling. Irrespective of Argos location class, we removed all extreme visual outliers (hundreds of km from the main data cluster) and for records with duplicate time stamps we removed the worse quality locations. We also removed all but the last location when the turtle was resident in the breeding area, as previously determined in Rees et al. (2025). We then performed state space modelling (SSM) on the pre-cleaned data in R (R Core Team 2024) using the package aniMotum (Jonsen et al. 2023). In aniMotum we set vmax (maximum travel speed) to 1.39 m s^{-1} (5 km h^{-1}) and selected the "rw" (random walk) model with a 12-hr time step.

To produce the final dataset, we removed all grossly outlying locations produced by the SSM together with multiple consecutive interpolated locations that were produced by the SSM when there was a gap greater than 7 days in the original Argos location data for any individual.

Mapping and post-SSM spatial data processing were undertaken in the Free and Open Source QGIS v3.40.4 (www.qgis.org). All summary statistics are presented as mean ± standard deviation.

Classification of movements and behaviours

Turtle behaviour was classified as migrating/remigrating, foraging or mixed behaviour based on sustained speed of travel and track tortuosity. Foraging periods were defined by slow rates of travel (< 1 km h^{-1}) with multidirectional movement. Migration/Remigration periods were defined by faster travel (> 1 km h^{-1}) with directed movement (*i.e.*, sections of track with low tortuosity) and mixed behaviour periods were defined by slow rates of travel (≤ 1 km h^{-1}) combined with directed movements and generally occurred in offshore locations. Short periods (≤ 3 d) of any one behaviour type during a protracted period of another behaviour type (*e.g.*, faster travel speeds in a period of mixed behaviour movement) were incorporated in the main behaviour type. Periods of foraging of 7 d or less during initial migrations were considered stopovers (see Cerritelli et al. 2022) and were not interpreted as the end of post-breeding migration.

If a turtle migrated to a spatially restricted identifiable foraging location it was classified as sedentary. If a turtle undertook long-term movements without establishing a clear restricted foraging location it was classified as Nomadic. Turtles that exhibited both behaviours were classified as semi-nomadic.

Analysis of the influence of foraging area and behaviour on turtle body size

To gain insight into the influence of foraging area (Adriatic, Aegean, Ionian/northern Libyan Sea and Tunisian shelf; see results) and foraging strategy (sedentary, semi-nomadic, nomadic) on body size we compared the mean CCL for each variable. Statistical comparisons were not undertaken due to small sample size.

Determining threat levels from fisheries

To examine the relative potential impact of fisheries on the turtles over their tracked range we obtained twelve months of contemporaneous fishing effort data from the Global Fishing Watch (GFW) web portal (Global Fishing Watch 2025). GFW fisheries effort data were determined from AIS (automatic identification system) data for vessels 15 m or longer with apparent fishing effort and gear type used identified by a neural network model (Kroodsma et al. 2018). Data were downloaded, in 0.1° cells, for the period September 2022 to August 2023; this date range covered a large period of tracking for the adult females and complete tracking of two of the three adult males.

RESULTS

The turtles

Average CCL was 83.1 cm (± 4.9, range 73.5–91.5 cm) for all 11 turtles, 82.0 cm (± 4.6, range 73.5–89.5 cm) for the 8 female turtles and 86.0 cm (±5.5, range 80.5–91.5 cm) for the 3 males (Table 1). Male turtle tail lengths were on average 22.8 cm (± 2.9, range 19.5–25.0 cm, n = 3). We received location data from all 11 turtles tracked between 2021 and 2023. The turtles were tracked for an average of 326.9 d. Females tended to be tracked for longer than males; 351.6 ± 232.9 d (range 69–716 d) and 261.0 ± 248.5 d (range 98–547 d), respectively (Table 2).

Table 1. Body size (and tail length of the tracked adult males), migratory speed, and foraging region and strategy for the 11 loggerhead sea turtles tracked after breeding in Kyparissia Bay. CCL = curved carapace length (notch to tip). TL = tail length (from innermost part of the notch between the supracaudal scutes and the tip of the extended tail)

Turtle	Sex	CCL (cm)	TL (cm)	Average migration speed (km h^{-1} ± SD)	Foraging region	Foraging strategy category
A	F	82.0	-	2.0 ±0.7	Aegean	Sedentary
B	F	73.5	-	1.3 ±0.6	Ionian/northern Libyan	Nomadic
C	F	80.0	-	1.6 ±0.4	Adriatic	Semi-nomadic
D	F	85.5	-	2.4 ±0.6	Tunisian shelf	Sedentary[a]
E	F	89.5	-	2.2 ±0.6	Ionian	Sedentary[b]
F	F	81.0	-	2.0 ±0.8	Ionian	Sedentary
G	F	83.0	-	1.8 ±0.6	Adriatic	Sedentary
H	F	81.5	-	1.8 ±0.6	Tunisian shelf	Sedentary
I	M	91.5	24.0	1.2 ±0.6	Aegean	Sedentary
K	M	86.0	25.0	1.6 ±0.5	Aegean	Sedentary
J	M	80.5	19.5	1.3 ±0.5	Ionian / Adriatic	Semi-nomadic

[a]Track stopped the day after the turtle arrived at the Libyan coast. [b]Gap of 194 d in tracking data after turtle reached its foraging area, with locations resuming in the same location afterwards.

Table 2. Summary data of the post-breeding tracking durations of the 11 loggerhead turtles tracked from Kyparissia Bay breeding area

Turtle	Deploy Date	Depart Date	Breeding duration	Arrival at foraging area	Migration duration	End date	Tracking duration
A	29/06/2021	21/07/2021	22	11/08/2021	21	02/01/2023	552
B	03/07/2021	23/07/2021	20	02/08/2021[a]	10	19/06/2023	716
C	04/07/2021	17/07/2021	13	10/08/2021	24	31/01/2022	211
D	09/06/2022	30/07/2022	51	17/08/2022	18	17/08/2022	69
E	12/06/2022	21/07/2022	39	29/07/2022	8	15/02/2023	248
F	12/06/2022	25/07/2022	43	02/08/2022	8	16/10/2023	491
G	13/06/2022	19/07/2022	36	17/08/2022	29	09/09/2022	88
H	13/06/2022	28/07/2022	45	19/08/2022	22	25/08/2023	438
I	02/05/2023	03/05/2023	1	14/06/2023	42	08/08/2023	98
K	03/05/2023	06/05/2023	3	23/05/2023	17	18/09/2023	138
J	03/05/2023	28/05/2023	25	01/06/2023[b]	4	31/10/2024	547

Turtle behaviour switched from migration to mixed[a] or foraging[b] for a period of 9 days or longer.

Duration and Speed of behaviours, migrations and movements

Females departed the breeding area on average 33.6 days after tagging (± 13.6, range 13–51 d, n = 8). Males departed 9.7 days after tagging (± 13.3, range 1–25 d, n = 3). Average migration duration lasted 17.5 d (± 8.0, range 8–29 d, n = 8) for female turtles and 21.0 d (± 19.3, range 4–42 days, n = 3) for males, which included stopovers of 4 and 7 d for two turtles (Table 2). Average mean migration speed for all turtles was 1.7 km h^{-1}. Average mean speed for females was 1.9 km h^{-1} (± 0.3, range 1.3–2.4 km h^{-1}, n = 8) and 1.3 km h^{-1} (± 0.2, range 1.2–1.6 km h^{-1}, n = 3) for males (Table 1).

Destinations and groupings

End points of the tracked turtles can be grouped into four distinct regions (Fig. 1, Table 1). The Aegean Sea was the end point for 3 turtles (*1f(A),2m(I,K)*; Fig. 1a), the Adriatic Sea was the end point for 3 turtles (*2f(C,G),1m(J)*; Fig. 1b) with one turtle spending an extended period in the Ionian Sea (J). The Ionian Sea was the end point for a further 3 turtles (*3f(B,E,F)*; Fig. 1c,d) and the Tunisian shelf was the end point for the final 2 turtles (*2f(D,H)*; Fig. 1e).

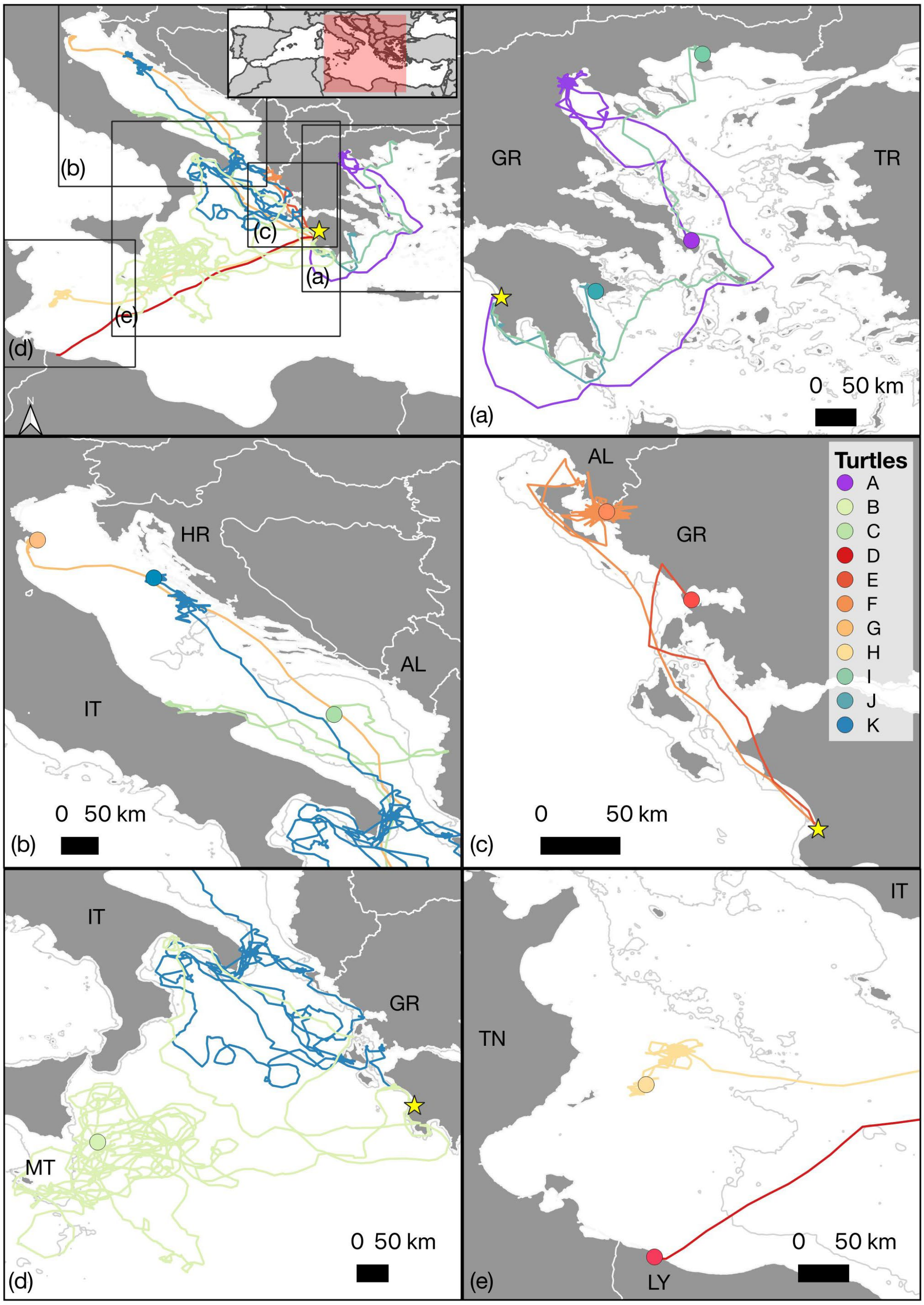

Fig. 1. Post-breeding migrations, movements and end points for the 11 loggerhead turtles tracked from Kyparissia Bay. (a) Aegean Sea, (b) Adriatic Sea, (c) Ionian Sea (sedentary turtles), (d) Ionian Sea/ northern Libyan Sea (nomadic turtles), and (e) Tunisian Shelf. The nomadic portion of the track ending in the Adriatic panel (b) is shown in panel (d). Grey line = 200 m isobath. Bathymetry representation is derived from GEBCO data (https://www.gebco.net/). Yellow star is the tagging site. Coloured circles are end points of each track.

Foraging strategy (sedentary or nomadic)

The turtles were also grouped by foraging strategy (Table 1). Six of the turtles were classified as sedentary, having established restricted area foraging sites in the Aegean (*1f(A),2m(I,K*), Adriatic (*1f(G)*), Ionian (*1f(F)*), and Tunisian shelf (*1f(H)*). One turtle remained nomadic in the Ionian/northern Libyan Sea region (*1f(B)*). Two turtles were semi-nomadic, with 1 (*1m(J)*) initially being nomadic until settling in the Adriatic, and the other (*1f(C)*) establishing a long-term coastal foraging site in the Adriatic before moving away and behaving nomadically in the same region for its final 20 days of tracking. The remaining two turtles were most likely also sedentary, as their tracks ended in shallow coastal waters, but the track stopped the day after reaching the Libyan coast for one (*1f(D)*) and the other track (*1f(E)*) contained a gap of almost 200 d before the final 7 d of tracking placed the turtle in the same restricted area of coast.

Influence of foraging strategy or region on body size

From the four identified foraging regions, on average the largest turtles were present in the Aegean (mean CCL = 86.5 cm, n = 3) followed by the Tunisian shelf (mean CCL = 83.5 cm, n = 2), and then the Adriatic and Ionian/northern Libyan Sea regions (mean CCL = 81.5cm, n = 2 and mean CCL = 81.3 cm, n = 3, respectively). One turtle was excluded from this assessment as it extensively used both the Adriatic and Ionian regions and could not be assigned to just one of them.

Based on foraging strategy, the largest turtles selected sedentary behaviour (mean CCL = 85.0 cm, n = 8), next largest were the semi-nomadic turtles (mean CCL = 80.3 cm, n = 2) and the only fully nomadic turtle was smallest (CCL = 73.5 cm, n = 1), at over 6 cm smaller than the next smallest turtle.

Fisheries threats

Fishing activity levels in the central Mediterranean, as derived from AIS data by GFW, showed several distinct large-scale hotspots (Fig. 2). Based on apparent fishery activity approaching or exceeding 3,000 hr within the sampled year, we can see that most of the neritic Adriatic Sea and much of the waters between Sicily and Tunisia/Libya were extensive areas of high levels of fishing activity. Other relevant areas included the coastal regions of the northern Ionian Sea and Thermaikos Gulf in the NW of the Aegean Sea (Fig. 2).

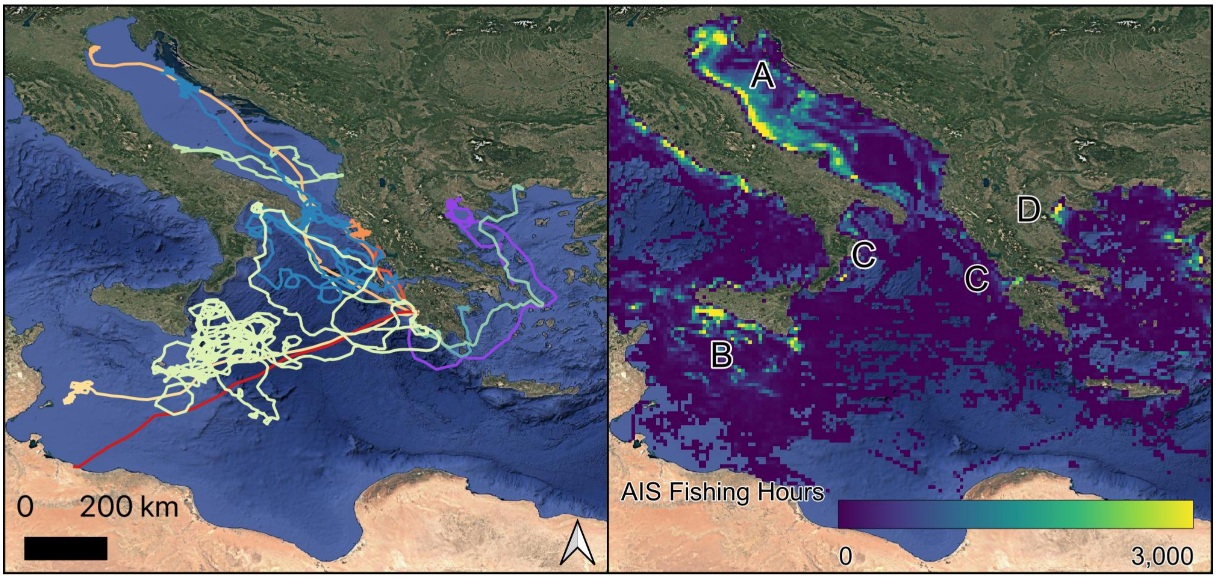

Fig. 2. Potential threat posed by fisheries to the loggerhead turtles tracked from Kyparissia Bay. Left panel: Tracks of the 11 adult loggerhead turtles equipped with Argos satellite transmitters in Kyparissia Bay, Greece. Right panel: Fishing effort in the same location in 0.1° cells, between September 2022 and August 2023. Fishing effort, determined from AIS data, downloaded from Global Fishing Watch (globalfishingwatch.com). Areas with 3,000 or more fishing hours are depicted in the same colour. Areas of high intensity fishing are evident in (A) neritic part of the Adriatic Sea, (B) between Sicily and Tunisia/Libya, (C) coastal regions of the Ionian Sea, and (D) Thermaikos Gulf in the NW of the Aegean Sea, which coincide with the turtle tracks.

DISCUSSION

Travel and speed in context

As expected, the overall migration speed demonstrated by the study turtles (1.7 km h^{-1}), was within the range published for other migrating adult loggerhead turtles in the Mediterranean (Godley et al. 2002; Schofield et al. 2010; Cerritelli et al. 2022). Their travels included ‘stop overs’ as found with turtles migrating from other Greek and Turkish nesting areas (Dujon et al. 2017; Cerritelli et al. 2022). However, the three male turtles average travel speed (1.3 km h^{-1}) was lower than other tracked turtles (females), even on their slower coastal migratory pathways, which averaged at 1.6 km h^{-1} (Godley et al. 2002; Cerritelli et al. 2022). It could be that adult male loggerheads migrate more slowly than adult females, but more turtles need to be tracked to confirm this difference is not simply an artefact of small sample size. Imprecision in travel speeds may result from the use of SSM generated locations at 12 hourly intervals, rather than raw tracking data over variable time spans to determine speed. This would especially impact periods where turtles were undertaking more than one of the assigned behavioural categories in a 12-hr window.

However, we consider the selected method sufficiently robust to provide biologically meaningful results.

Destinations compared to previous findings

The majority of the study turtles migrated to the northern Ionian and Adriatic Seas (Fig. 1, Table 1), which are the highest use adult locations previously identified from tag returns (Margaritoulis et al. 2007) and tracking of Laganas Bay turtles (Zbinden et al. 2011, Schofield et al. 2013a). The Tunisian shelf is underrepresented in this study (*n* = 2) compared to the previous works focussing on Laganas Bay turtles (Margaritoulis et al 2007, Schofield et al 2013a) that found that region to hold the second largest number of turtles. The final turtles in this study migrated to the Aegean Sea with one more turtle heading there than the Tunisian shelf (*n* = 3). These results better align with the tag return data of Margaritoulis et al. (2007), which includes Kyparissia Bay tagged turtles, than the tracking results of Laganas Bay turtles (Schofield et al 2013a). Nesting females from Kyparissia have also been reported to migrate into the Western Mediterranean (Backof 2013; Haywood et al. 2021) but none from the current study did so. Separation of tag return data, such as presented by Margaritoulis et al. (2007), per nesting site and increasing the sample size of tracked turtles from Kyparissia Bay can support or refute any differences in the proportions of turtles migrating to the different regions and potentially provide additional evidence for the different conservation status between the two nesting aggregations (Margaritoulis et al. 2025).

There are potentially up to 2,000 nesting turtles in a single year in Kyparissia Bay—based on clutch frequency of ~3.5 (Rees et al. 2023) and 8,019 nests in the updated core nesting area in 2024 (Margaritoulis et al. 2025). In addition, there will be a large cohort of breeding males present in the area. Consequently, the number of turtles tracked here (*n* = 11) needs to be increased dramatically to provide more conclusive population-level results. Furthermore, tracking turtles from additional seasons may reveal any interannual variation in migratory destinations and overcome limitations of the potentially biased tag return data and the limited temporal spread of the current tracking study.

Increasing the sample of turtles tracked to identify foraging areas and strategies may be achieved through a combination of ways. Emerging alternative technologies, such as transmitters using the Iridium satellite system (Cerritelli et al. 2022; Lamont et al. 2024) or the cellular phone GSM network (Rees et al. 2023), which may result in lower costs per tracked individual, may help stretch funding to track larger numbers of turtles. Furthermore, compilation of all existing tracking data into a single meta-analysis (*e.g.*, Ferreira et al. 2021) would strengthen findings in terms of relative abundance of turtles in the foraging areas and give indication of the diversity of turtles from different breeding populations that utilise these areas.

SIA using carbon, nitrogen and sulphur isotopes present in turtle epidermis tissue, whilst cheaper per individual than typical satellite tracking, has proven to be largely ineffective at differentiating many Mediterranean loggerhead foraging areas (Haywood et al. 2020 2021). However, the use of other isotopes such as oxygen, in commensal barnacles present on the turtles' carapaces may reveal insights into their spatial origins (Pearson et al. 2019) and should be explored further within the Mediterranean.

Behaviour and the established sedentary foraging paradigm

Three of the study turtles (B,C,J; 27%) did not follow the classic paradigm that post-breeding loggerhead turtles migrate to specific neritic areas and establish spatially distinct foraging sites (see Schofield et al. 2010, 2013a and Mingozzi et al. 2016 for examples) but instead exhibited prolonged periods of nomadic behaviour in both neritic and oceanic waters. The most extreme example of this behaviour pattern was shown by turtle B (Fig. 1d). It moved from near to eastern Sicily, to the southern mainland Italian coast and back to Kyparissia Bay and then once more to the western Ionian, without breeding, for ~700 days. Although apparently rare, this type of behaviour has been reported before from Kyparissia, with adult female turtles remaining nomadic in the western Mediterranean (Haywood et al. 2021). Additionally, a single adult female from 17 (6%) tracked after nesting in southwestern Türkiye undertook wandering movements and established two large-scale foraging areas in the western Ionian and Adriatic Seas (Cerritelli et al. 2022). Two turtles from 37 (5%) tracked from Cyprus also remained nomadic; one also inhabiting the northern Ionian sea and the other spending time over the Tunisian Plateau before covering hundreds of kilometres moving around in oceanic waters of the southern Western Mediterranean (Haywood et al. 2020). These low frequency occurrences of nomadism contrast with a study of sub-adult and adult loggerheads obtained in the Tyrrhenian Sea where 6 of 8 turtles (75%) undertook long-distance circuitous movements in the oceanic environment (Luschi et al. 2017). From the above findings, either a size-based ontogenetic change in behaviour or a temporally evolved behaviour where the nomadic life-history pattern is becoming more prevalent may be inferred.

Area / behaviour influence on body size

The fully nomadic turtle in this study was by far the smallest turtle tracked, and the semi nomadic turtles the next smallest. This suggests a notable carryover effect of a nomadic foraging strategy, possibly in combination with the selected foraging region, as has been shown for loggerhead turtles in the northwest Atlantic (Ceriani et al 2015). For foraging strategy and location to influence body size, a turtle would need to show consistent behaviour over successive years. Though we have only one period for the turtle in this study, other studies show that turtles show fidelity to foraging areas and resulting foraging strategy (Broderick et al. 2007; Schofield et al. 2010; Rees and Margaritoulis 2024) and a persistent long-term nomadic foraging strategy can be assumed for the turtle.

Previous studies on nesting Mediterranean loggerheads have revealed a north-south dichotomy in turtle size, with northern turtles being larger (Zbinden et al. 2011; Cardona et al. 2014; Patel et al. 2015; Haywood et al. 2020) and laying larger clutches (Zbinden et al. 2011; Cardona et al. 2014; Patel et al. 2015). These effects were attributed to better quality benthic forage in the north. Those results contrast with our findings that suggest foraging strategy plays a more important role in body size than foraging location. No reference to a relationship between size and foraging strategy of the nesting females was made in any of the previous Mediterranean studies. Both Zbinden et al. (2011) and Patel et al. (2015) present tracks of turtles that only established restricted benthic foraging areas and lacked any nomadic individuals. The nomadic turtles from Haywood et al. (2020) were of similar small size to other tracked individuals, thus our finding of a small nomadic foraging in the Ionian/northern Libyan Sea is a novel result and worthy of further investigation through tracking other small conspecifics from the area.

Interpretation of the influence of foraging area and strategy on body size may be confounded by the inclusion of both male and female turtles in the analysis, with male turtles in this study being on average larger than their female conspecifics. However, another study in the Mediterranean revealed no sexually dimorphic body size differences (Schofield et al. 2013a), hence the influence of foraging strategy is likely to be the primary driver in differential body size.

Other studies with loggerheads breeding at Cape Verde and Japan have shown that adults turtles residing in oceanic conditions were smaller than their conspecifics feeding in neritic habitats (Hatase et al. 2002, Hawkes et al. 2006), which is reflected in the results of this study. Furthermore, at least for the Cape Verdean turtles, the oceanic residents also remained nomadic for the duration of their tracking, which again is a behaviour presented by the turtles that were either semi-nomadic or nomadic in this study. We would suggest that long-term presentation of a foraging strategy (nomadic vs sedentary) is a result of foraging habitat (benthic or midwater) selection and results in measurable differences in body size between the two categories of animals.

Threat impacts

The factors driving the different turtle behaviour result in individuals being exposed to varying levels of anthropogenic threats. The most insidious marine threat to sea turtles is bycatch in fisheries (Wallace et al. 2025) with the most recent estimate indicating over 120,000 turtles per year end up as bycatch per year in the most important fishery types across the Mediterranean (Lucchetti 2021). Fishing intensity is not uniform across the Mediterranean, with, for example, certain large-scale areas such as the Adriatic Sea, parts of the shelf seas between Sicily and Tunisia and sections of the Aegean Sea experiencing widescale intensive fishing (Fig. 2). These are three of the regions identified here as preferred foraging grounds for loggerhead turtles nesting in Kyparissia and results in the turtles experiencing high fisheries pressure whilst away from their breeding grounds. The smaller nomadic turtle would consequently be least affected by bottom gears but would be affected by other fishing taking place in more offshore oceanic waters.

It should be noted that fishing activity distribution maps derived solely from AIS data (such as shown in Fig. 2) are prone to underreporting vessel presence in certain locations where there are no AIS receivers or when AIS transmitters are muted. In the Mediterranean this occurs most frequently in the south leading to the underreporting of fishing activity, for example, in Tunisian waters (Fig. 2). However, through inclusion of SAR (synthetic aperture radar) data a high presence of fishing vessels is shown in Tunisian coastal waters and shelf sea (Marsaglia et al. 2024; Fig. 3), indicating the entire region poses high risk to turtles foraging there.

Each life history and behavioural variation for loggerheads comes with its own raft of ecological trade-offs that can impact fecundity and survivorship. Conservation measures to reduce bycatch and improve the outcome for bycaught turtles continue to be priority actions away from nesting areas. The greater our knowledge of migratory routes and foraging hotspots, as determined through tracking studies such as this one, the more targeted and impactful such measures may be.

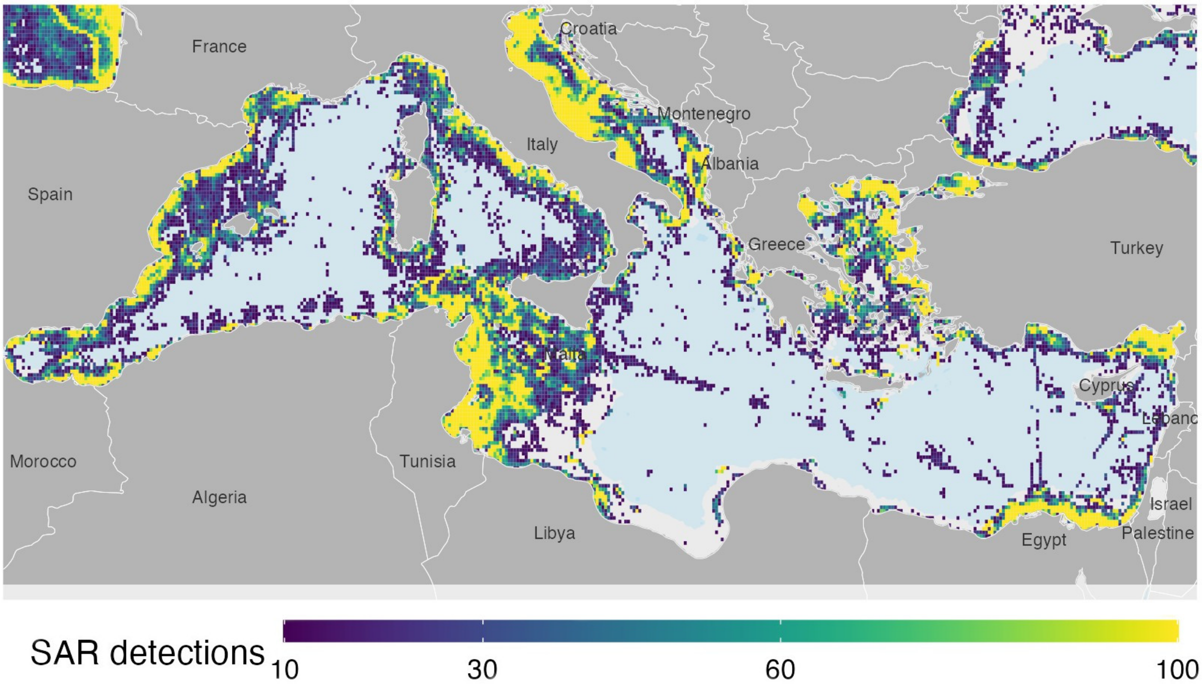

Fig. 3. "SAR fishing vessel presence from Global Fishing Watch SAR data from 2017 to 2021 aggregated by number of fishing vessel detections in 0.1 decimal degrees cells. The light blue shaded area represents the areas with depths greater than 1,000 m". Reproduced from Marsaglia et al. (2024) under Creative Commons Attribution License 4.0.

CONCLUSIONS

Although there are alternative ways of determining high-use areas by sea turtles, such as combining analysis of aerial and boat transect data with environmental data (DiMatteo et al. 2022, 2024), satellite telemetry remains the best method. The benefits include determining routes of individual turtle migrations, identifying the origins of turtles in a location where the turtles cannot be accessed to read flipper tags, and revealing nesting-site specific hotspots.

Limited tracking of breeding turtles in this study has confirmed foraging sites that have previously been indicated from flipper tag returns. However, given that SIA is not currently able to distinguish specific foraging regions for Mediterranean loggerheads (Zbinden et al. 2011, Haywood et al. 2020, Haywood et al. 2021) a larger sample of tracked turtles is needed to support population level inferences on foraging hotspot distribution.

Likewise, additional tracking combined with tracked-turtle individual nesting histories should be used to further elucidate the interplay of foraging strategy and location with body size and fecundity as suggested in other studies (Zbinden et al. 2011, Cardona et al. 2014, Patel et al. 2015).

Despite the limited sample size, present data support previous findings as to the distribution of adult loggerhead turtles away from the breeding areas. This strengthens the need for adoption of suitable bycatch reduction measures, such as gear or fishing method modifications or spatial and temporal closures, which will improve the conservation status of turtles in the respective areas.

Acknowledgments: Satellite tracking was funded by NCC in the context of the Biodiversity Monitoring and Critical Habitats Assessment project undertaken for HELLENiQ UPSTREAM S.A. The authors wish to thank ARCHELON, the Sea Turtle Protection Society of Greece, for field support, using personnel from their on-going sea turtle nest monitoring and conservation program in the area to assist with locating nesting turtles and deploying transmitters. We also thank members of BIOTOPIA and Mom (the Hellenic Society for the study and protection of the Monk Seal) who assisted with capture of the male turtles tracked in this study.

Authors' contributions: AFR: Conceived study, undertook fieldwork, curated and analysed data, wrote initial draft of the manuscript. TD: Conceived the study, undertook fieldwork, contributed to drafting the manuscript and approved its final submitted version., YV and GM: Conceived the study, contributed to drafting the manuscript and approved its final submitted version.

Competing interests: HELLENiQ UPSTREAM S.A. funded wildlife research in the Kyparissia Bay region as part of its commitment to conservation while undertaking surveys for potential exploration and exploitation of hydrocarbons in Kyparissiakos Bay.

Availability of data and materials: Raw tracking data analysed in this paper are available from the authors upon reasonable request and can be used with citation of this publication in the resulting documents/outputs.

Ethics approval consent to participate: Interactions with and tagging the turtles were covered under permit YPEN/DDD/26967/698 from the Ministry of Environment. Tagging and measuring turtles followed internationally accepted standards.

REFERENCES

Backof TF. 2013. Tracking and analysis of the spatial and thermal habitats of inter-nesting loggerheads (*Caretta caretta*) in Kyparissia Bay, Greece. MSc Thesis, Pudue University, Indiana, USA.

Baldi G, Furii G, Del Vecchio M, Salvemini P, Vallini C et al. 2023. Behavioural plasticity in the use of a neritic foraging area by loggerhead sea turtles: insights from 37 years of capture–mark–recapture in the Adriatic Sea (Mediterranean Sea), ICES J Mar Sci **80:**210–217. doi:10.1093/icesjms/fsac227.

Bolten AB. 1999. Techniques for measuring sea turtles. *In*: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp110–114.

Bowen BW, Karl SA. 2007. Population genetics and phylogeography of sea turtles. Molec Ecol **16:**4886–4907. doi:10.1111/j.1365-294X.2007.03542.x.

Bradshaw PJ, Broderick AC, Carreras C, Inger R, Fuller W et al. 2017. Satellite tracking and stable isotope analysis highlight differential recruitment among foraging areas in green turtles. Mar Ecol Prog Ser **582:**201–214. doi:10.3354/meps12297.

Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ. 2007. Fidelity and over-wintering of sea turtles. Proc R Soc B **274:**1533–1539. doi:10.1098/rspb.2007.0211.

Cardona L, Clusa M, Eder E, Demetropoulos A, Margaritoulis D et al. 2014. Distribution patterns and foraging ground productivity determine clutch size in Mediterranean loggerhead turtles. Mar Ecol Prog Ser **497:**229−241. doi:10.3354/meps10595.

Ceriani SA, Roth JD, Evans DR, Weishampel JF, Ehrhart LM. 2012. Inferred foraging areas of loggerhead turtles using satellite telemetry and stable isotopes. PLoS ONE **7:**e45335. doi:10.1371/journal.pone.0045335.

Ceriani SA, Roth JD, Tucker AD, Evans DR, Addison DS et al. 2015. Carry-over effects and foraging ground dynamics of a major loggerhead breeding aggregation. Mar Biol **162:**1955−1968. doi:10.1007/s00227-015-2721-x.

Cerritelli G, Casale P, Sözbilen D, Hochscheid S, Luschi P et al. 2022. Multidirectional migrations from a major nesting area in Turkey support the widespread distribution of foraging sites for loggerhead turtles in the Mediterranean. Mar Ecol Prog Ser **683:**169–177. doi:10.3354/meps13946.

CLS (Collecte Localisation Satellites). 2016. Argos User's Manual. Available at: https://www.argos-system.org/support/. (Accessed 17 May 2025)

Coffee OI, Booth DT, Thia JA, Limpus CJ. 2020. When isotopes fail: importance of satellite telemetry and multi-site validation when estimating the foraging grounds of migratory species. Mar Ecol Prog Ser **633:**197–206. doi:10.3354/meps13179.

DiMatteo A, Cañadas A, Roberts J, Sparks L, Panigada S et al. 2022. Basin-wide estimates of loggerhead turtle abundance in the Mediterranean Sea derived from line transect surveys. Front Mar Sci **9:**930412. doi:10.3389/fmars.2022.930412.

DiMatteo A, Roberts JJ, Jones D, Garrison L, Hart KM et al. 2024. Sea turtle density surface models along the United States Atlantic coast. Endanger Species Res **53:**227–245. doi:10.3354/esr01298.

Dujon AM, Schofield G, Lester RE, Esteban N, Hays GC. 2017. Fastloc-GPS reveals daytime departure and arrival during long-distance migration and the use of different resting strategies in sea turtles. Mar Biol **164:**187. doi:10.1007/s00227-017-3216-8.

Ehrhart LM, Ogren LH. 1999. Studies in foraging habitats: capturing and handling turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp61–64.

Ferreira LC, Thums M, Fossette S, Wilson P, Shimada T et al. 2021. Multiple satellite tracking datasets inform green turtle conservation at a regional scale. Divers Distrib **27:**249–266. doi:10.1111/ddi.13197.

Global Fishing Watch. 2025. Global AIS-based apparent fishing effort dataset, Version 3.0. https://doi.org/10.5281/zenodo.14982712.

Godley BJ, Richardson S, Broderick AC, Coyne MS, Glen F et al. 2002. Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecography **25:**352–362. doi:10.1034/j.1600-0587.2002.250312.x.

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH et al. 2008. Satellite tracking of sea turtles: Where have we been and where do we go next? Endanger Species Res **4:**3–22. doi:10.3354/esr00060.

Hatase H, Takai N, Matsuzawa Y, Sakamoto W, Omuta K et al. 2002. Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. Mar Ecol Prog Ser **233:**273–281. doi:10.3354/meps233273.

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Lopez-Jurado L-F et al. 2006. Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. Curr Biol **16:**990–995. doi:10.1016/j.cub.2006.03.063.

Hays GC, Mazaris AD, Schofield G. 2014. Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. Front Mar Sci **1:**43. doi:10.3389/fmars.2014.00043.

Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM et al. 2016. Key questions in marine megafauna movement ecology. Trends Ecol Evol **31**(6)**:**463–475. doi:10.1016/j.tree.2016.02.015.

Haywood JC, Fuller WJ, Godley BJ, Margaritoulis D, Shutler JD et al. 2020. Spatial ecology of loggerhead turtles: Insights from stable isotope markers and satellite telemetry. Divers Distrib **26**(3)**:**368–381. doi:10.1111/ddi.13023.

Haywood J, Margaritoulis D, Theodorou P, Rees AF. 2021. Identifying critical marine habitats of the largest nesting population of loggerhead sea turtles in the Mediterranean: insights from stable isotope markers and satellite telemetry. Testudo **9:**80–88.

Jonsen ID, Grecian WJ, Phillips L, Carroll G, McMahon C et al. 2023. aniMotum, an R package for animal movement data: Rapid quality control, behavioural estimation and simulation. Methods Ecol Evol **14:**806–816. doi:10.1111/2041-210X.14060.

Kroodsma DA, Mayorga J, Hochberg T, Miller NA, Boerder K et al. 2018. Tracking the global footprint of fisheries. Science **359**:904–908. doi:10.1126/science.aao5646.

Lamont MM, Slone D, Reid J, Butler SM, Alday J. 2024. Deep vs shallow: GPS tags reveal a dichotomy in movement patterns of loggerhead turtles foraging in a coastal bay. Mov Ecol **12:**40. doi:10.1186/s40462-024-00480-y.

Limpus CJ, Miller JD, Parmenter CJ, Reimer D, McLachland N et al. 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. Wildl Res **19:**347–358.

Lucchetti A. 2021. Sea turtles. In Carpentieri P, Nastasi A, Sessa M, Srour A (eds) Incidental catch of vulnerable species in Mediterranean and Black Sea fisheries – A review. Studies and Reviews No. 101 (General Fisheries Commission for the Mediterranean). Rome, FAO. doi:10.4060/cb5405en.

Luschi P, Mencacci R, Cerritelli G, Papetti L, Hochscheid S. 2017. Large-scale movements in the oceanic environment identify important foraging areas for loggerheads in central Mediterranean Sea. Mar Biol **165:**4. doi:10.1007/s00227-017-3255-1.

Margaritoulis D, Koutsodendris A, Panagopoulou A. 2007. Fisheries interactions with marine turtles. In: Papaconstantinou C, Zenetos A, Vassilopoulou V, Tserpes G (eds) State of Hellenic Fisheries. Hellenic Centre for Marine Research Publications, Athens, Greece, pp279–286.

Margaritoulis D, Rees AF, Riggall TE. 2025. Exponential increase in a loggerhead sea turtle nesting population: Investigating the role of multi-decadal nest protection in Kyparissia Bay, Greece. Zool Stud **64:**29. doi:10.6620/ZS.2025.64-29.

Marsaglia L, Parisi A, Libralato S, Miller NA, Davis P et al. 2024. Shedding light on trawl fishing activity in the Mediterranean Sea with remote sensing data. ICES J Mar Sci **82**(2)**:**fsae153. doi:10.1093/icesjms/fsae153.

Miller JD. 1997. Reproduction in sea turtles. *In*: Lutz PL, Musick JA (eds) The Biology of Sea Turtles. CRC Press, pp51–81.

Mingozzi T, Mencacci R, Cerritelli G, Giunchi D, Luschi P. 2016. Living between widely separated areas: Long-term monitoring of Mediterranean loggerhead turtles sheds light on cryptic aspects of females spatial ecology. J Exp Mar Biol Ecol **485:**8–17. doi:10.1016/j.jembe.2016.08.007.

Mortimer JA, Carr A. 1987. Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). Copeia **1987:**103–113. doi:10.2307/1446043.

Musick JA, Limpus CJ. 1997. Habitat utilization and migration in juvenile sea turtles. *In*: Lutz PL, Musick JA (eds) The Biology of Sea Turtles. CRC Press, pp. 137–163.

Omeyer LCM, Stokes KL, Beton D, Çiçek BA, Davey S et al. 2021. Investigating differences in population recovery rates of two sympatrically nesting sea turtle species. Anim Cons **24:**832–846. doi:10.1111/acv.12689.

Patel SH, Panagopoulou A, Morreale SJ, Kilham SS, Karakassis I et al. 2015. Differences in size and reproductive output of loggerhead turtles *Caretta caretta* nesting in the eastern Mediterranean Sea are linked to foraging site. Mar Ecol Prog Ser **535:**231–241. doi:10.3354/meps11433.

Pearson RM, van de Merwe JP, Gagan MK, Limpus CJ, Connolly RM. 2019. Distinguishing between sea turtle foraging areas using stable isotopes from commensal barnacle shells. Sci Rep **9:**6565. doi:10.1038/s41598-019-42983-4.

Pilcher NJ, Antonopoulou M, Perry L, Abdel-Moati MA, Al Abdessalaam TZ et al. 2014. Identification of Important Sea Turtle Areas (ITAs) for hawksbill turtles in the Arabian Region. J Exp Mar Biol Ecol **460:**89–99. doi:10.1016/j.jembe.2014.06.009.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Rees AF, Margaritoulis D. 2024. No place like home: Records of a male loggerhead sea turtle in a Greek foraging ground spanning 18 years. MedTurtle Bulletin **5:**15–19.

Rees AF, Al Saady S, Broderick AC, Coyne MS, Papathanasopoulou N et al. 2010. Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*. Mar Ecol Prog Ser **418:**201–212. doi:10.3354/meps08767.

Rees AF, Papathanasopoulou N, Papoulias P, Samlidou G, Theodorou P et al. 2023. Internesting habitat preference and updated clutch frequency values for loggerhead turtles (*Caretta caretta*) nesting in Kyparissia Bay, Greece. Herp Cons Biol **18:**551–559.

Rees AF, Dimalexis T, Mikoniatis G, Vavassis Y. 2025. Further evidence supporting internesting habitat boundaries for loggerhead turtles nesting in Kyparissia Bay, Greece. MedTurtle Bulletin **7:**29–33.

Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA et al. 2010. Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers Distrib **16:**840–853. doi:10.1111/j.1472-4642.2010.00694.x.

Schofield G, Dimadi A, Fossette A, Katselidis KA, Koutsoubas D et al. 2013a. Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. Divers Distrib **19:**834–844. doi:10.1111/ddi.12077.

Schofield G, Scott R, Dimadi A, Fossette S, Katselidis KA et al. 2013b. Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. Biol Cons **161:**101–109. doi:10.1016/j.biocon.2013.03.004.

Shimada T, Limpus CJ, Hamann M, Bell I, Esteban N et al. 2019. Fidelity to foraging sites after long migrations. J Anim Ecol **89:**1008–1016. doi:10.1111/1365-2656.13157.

Wallace BP, Heppell SS, Lewison RL, Kelez S, Crowder LB. 2008. Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses. J Applied Ecol **45:**1076–1085. doi:10.1111/j.1365-2664.2008.01507.x.

Wallace BP, Posnik ZA, Hurley BJ, DiMatteo AD, Bandimere A et al. 2023. Marine turtle regional management units 2.0: an updated framework for conservation and research of wide-ranging megafauna species. End Species Res **52:**209–223. doi:10.3354/esr01243.x.

Wallace BP, Bandimere AN, Abreu-Grobois FA, Acosta H, Akiti J et al. 2025. Updated global conservation status and priorities for marine turtles. End Species Res **56:**247–276. doi:10.3354/esr01385.

Whittock PA, Pendoley KL, Hamann M. 2016. Flexible foraging: Post-nesting flatback turtles on the Australian continental shelf. J Exp Mar Biol Ecol **477:**112–119. doi:10.1016/j.jembe.2016.01.015.

Zbinden JA, Aebischer A, Margaritoulis D, Arlettaz R. 2008. Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. Mar Biol **153:**899–906. doi:10.1007/s00227-007-0862-2.

Zbinden JA, Bearhop S, Bradshaw P, Gill B, Margaritoulis D et al. 2011. Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. Mar Ecol Prog Ser **421:**291–302. doi:10.3354/meps08871.