

Living between widely separated areas: long-term monitoring of Mediterranean loggerhead turtles sheds light on cryptic aspects of females spatial ecology

Toni Mingozi¹ · Resi Mencacci² · Giulia Cerritelli² · Dimitri Giunchi² · Paolo Luschi²

¹ DiBEST, Department of Biology, Ecology and Earth Sciences, University of Calabria, Rende Italy. E-mail: antonio.mingozi@unical.it; Phone +39.0984.492979; Fax +39.0984.492946.

² Department of Biology, University of Pisa, Pisa, Italy

Abstract

Over the last decades, satellite tracking techniques have substantially advanced our understanding of sea turtle spatial behaviour, especially for the post-nesting migrations of females. Substantial gaps remains in our knowledge of the turtle behaviour during the remaining inter-reproductive period, that spans over 2-3 years. We report the results of a prolonged tracking experiment on loggerhead turtles nesting along the Ionian Calabria, the main breeding ground in Italy. Argos satellite transmitters were deployed on eight females, a sample representing a substantial fraction of the overall population (20-25 nesting females). All turtles but one were tracked for more than 300 days (range: 313-1523 days), revealing their spatial behaviour during a complete reproductive cycle and providing novel information on a number of poorly-known aspects of loggerhead spatial ecology: i) the post-nesting migratory strategy resulted in

accordance with that of most adult loggerheads tracked so far, as the nine routes of six turtles were directed towards specific sites all located in the Tunisian continental shelf, a main foraging area for Mediterranean turtles; ii) the pre-breeding migratory routes were rather variable, likely deriving from different navigational strategies adopted by migrating turtles, and their temporal pattern indicates that mating occurred away from the nesting area; iii) the 10 inter-nesting movements of four turtles revealed unusual long-distance loops mostly in oceanic waters (median of maximum distance from nesting location: 145.5 km); iv) while at the foraging grounds, four turtles occupied distinct areas during summer and winter, making directed movements between the two sites, seasonal core areas were separated and their size was larger in winter than in summer (median: 498 km² vs. 258 km²); v) individual females displayed a high fidelity to both sites in successive years. These findings further highlight the plasticity in loggerhead spatial behaviour and the importance of the Central Mediterranean and of the Tunisian shelf for loggerhead conservation.

Keywords: *Caretta caretta*, satellite tracking, migration, home range, individual plasticity, Mediterranean.

1. Introduction

Measures of effective conservation are particularly challenging for migratory species, both terrestrial (e.g. Piersma and Baker 2000; Bolger et al. 2008), and marine (e.g., Reynolds and Jennings 2000; Palumbi 2004). Actually, three relevant key facts are known to be critical for successful conservation planning (Bolger et al. 2008; Wilcove and Wikelski 2008): i) even the

largest protected areas are currently too small for wide-ranging species; ii) large-scale movements may extend over different countries therefore implying different conservation policies; iii) the detailed knowledge of migratory routes are essential in order to understand demographic connectivity between widely separated areas. Various examples of how movement data of terrestrial or marine animals were used to drive conservation efforts are provided by Hays et al. (2016).

Many animals spend a relevant part of their life moving over widely different spatial and temporal scales (Hansson and Akesson 2014). Therefore, the types of movements may differ even dramatically, but three main forms at least are normally recognized (Forman and Godron 1986; Sinclair et al. 2006; Hansson and Akesson 2014): local movement (within a home range, i.e. area daily covered for feeding and other activities), dispersal movement (one-way movement of an individual away from the area of birth or residence), and migration (cyclic movement of animal populations between two different areas/habitats during different seasons).

Our understanding of the spatio-temporal distribution, migratory connectivity and habitat use of wide-ranging species has dramatically increased over the last 30 years, thanks to a variety of technological tools such as satellite telemetry, genetic analyses, remote sensing and biochemical markers (e.g. Mills 2007; Hart and Hyrenbach 2009; Hawkes et al. 2011; Hays et al. 2016).

Sea turtles are the only reptiles that undertake large-scale migrations comparable of those of other terrestrial or marine vertebrates (Plotkin 2003; Southwood and Avens 2010). In most species, wide-ranging movements occur among different developmental habitats during the early life stages (Musick and Limpus 1997), while adults shuttle between distinct foraging and nesting grounds, often embarking in long-distance migrations on a multi-annual basis (Plotkin, 2003; Godley et al. 2008). Moreover, in some species adult females are known to perform extensive movements also between successive nesting events within the same breeding season, during the so-called internesting period (Godley et al. 2008).

Over the last few decades, satellite tracking techniques have led to substantial advances in the scientific knowledge of sea turtle spatial behaviour, revealing the movement patterns displayed by medium- to large- sized individuals (i.e., from late juveniles to adults), and also to obtain some indications on those of smaller juveniles (Mansfield et al. 2014). The picture provided by satellite tracking findings is still somewhat incomplete, even for the best documented case of adult females. The findings obtained are indeed biased towards the post-nesting migrations, that are typically tracked for some months after departure from the nesting area. What the females do for the rest of the inter-reproductive period, that spans over 2-3 years, is much less documented (Godley et al. 2008). In hard-shelled species, the turtle behaviour during the successive prolonged stay in neritic foraging area(s), as well as during the pre-breeding migrations, has been monitored in a minority of cases, such as in hawksbills (*Eretmochelys imbricata*; Hawkes et al. 2012) and loggerheads (*Caretta caretta*; Zbinden et al. 2008; Marcovaldi et al. 2010). This bias leaves out a most relevant part of the adult cycle, and the available findings thus only provide a sort of snapshot of the spatial behaviour of females throughout their 2-3 years reproductive cycle, limited to the first months after nesting.

The loggerhead is the most common sea turtle in the Mediterranean Sea (Casale and Margaritoulis 2010). Adults and juveniles occur throughout the entire basin, although nesting beaches are concentrated in the eastern basin, in particular along the Greek, Turkish and Cyprian coasts, for an average of over 7200 documented nests/years (Casale and Margaritoulis 2010). Recent genetic studies (mtDNA sequences) showed a degree of isolation among the Mediterranean rookeries, indicating the existence of distinct demographic sub-population, as a result of at least two colonisation events from the Atlantic (Clusa et al. 2013). Satellite tracking findings have started to outline an overall picture of the main movement patterns of these turtles, although some biases remains given that most efforts have focused on the adults of the main rookeries in Greece and Cyprus (Luschi and Casale 2014).

The Ionian coast of Calabria is currently recognized as the most important regular nesting ground of loggerhead turtle in Italy (Mingozzi et al. 2007), accounting for about 50-80% (average 65%) of the total nesting events documented countrywide with a total of 261 nests recorded in the period 2005-2014), that corresponds to a density of 12 to 27 nests/year. Nests are mostly concentrated (about 80% on average) along the southernmost Ionian coastline, the so-called “*Costa dei Gelsomini*” (Mingozzi unpubl data). Such a picture classifies the Ionian Calabrian coast as a marginal nesting ground for Mediterranean loggerhead turtles when compared with the other rookeries, hosting a small percentage of the total breeding events, and being located at the western limits of the Mediterranean regular nesting range of the species. Marginal populations are however relevant for species conservation, as they can significantly contribute to the overall genetic diversity (Lesica and Allendorf 1995; Eckert et al. 2008), and so information on the movement patterns shown in these cases is most valuable.

In the present paper we report the results of a prolonged tracking experiment on female loggerhead turtles nesting in Southern Italy, which constitutes the first tracking attempt on nesting females in Italy. The study aims to complement the available information on the movements of loggerhead females in the Mediterranean and in particular to: a) identify the spatial and temporal patterns of female migratory routes, both after and before breeding; b) identify foraging and wintering areas where the turtles stay during the non-breeding period; c) assess their fidelity to migratory routes and feeding grounds in subsequent years; d) to compare the movement patterns recorded during inter-nesting and migration with those described elsewhere. Such information is essential to contribute to the conservation planning of this endangered and marginal nesting population.

2. Materials and methods

2.1. Study area

The study area is located along the Ionian coast of Calabria, the southernmost part of the Italian Peninsula (Fig. 1), extending for 40.4 km between Capo Bruzzano (38.040°N, 16.145°E) and Melito di Porto Salvo (37.918°N; 15.788°E). For most part (86.2%, 34.8 km), the coast is constituted by low-lying sandy or sandy-shingly beaches, on average 28.9 ± 11.5 m wide (range: 5-70 m, $n = 346$), that provide an habitat potentially suitable for turtle nesting. The remaining 13.8% (5.5 km) is represented by highly eroded coast.

2.2. Satellite transmitter attachment

During four nesting seasons (years 2009, 2010, 2011, 2013), seven Platform Transmitter Terminals (PTTs) linked to Argos system (www.argos-system.org), were deployed on female loggerheads nesting along the study area. An eighth PTT was deployed on a large female (73 cm curved carapace length) found at night on a beach. Since no indication about nesting attempts was available for this turtle, it will not be considered in this analysis. Details on tracked turtles, transmitter models and deployment locations can be found in Tab. 1.

Taking into account the wide extent of potential nesting beaches, and therefore the inability to monitor the entire beach length during the night, an opportunistic searching method to locate nesting turtles was set up. Nighttime patrolling activity was concentrated on selected beach sectors only, where (and when) one or more failed nesting attempts were recorded during patrols conducted the previous morning. Night monitoring (from 10:00 p.m. to 04:00 a.m.) was carried out by at least two patrols equipped with night vision scope (Wild Heerbrugg Mod. Big 3), and long range torches (Mag Charger Mod. Rn4019e) which monitored a stretch of about 10-15 km around the selected beach.

Turtles were approached at the end of egg-laying process or after a false crawl, and PTTs were attached to their carapace by using standard gluing methods with epoxy resins (Powerfast Pure 2K, Powers Fasteners, Inc., Brewster, NY). Turtle Zeffiria (2009) was missing a part of the right rear flipper and, after several attempts, could not dig the egg chamber.

2.3. Location data analysis

We obtained the initial Argos data through STAT (Satellite Tracking and Analysis Tool, Coyne and Godley 2005), available on www.seaturtle.org. The locations obtained from Argos were subjected to a filtering process excluding locations that were considered invalid on the basis of a pre-determined speed threshold. Speed thresholds were determined individually, calculating for each female the maximum speed recorded between high-accuracy localizations (Argos location classes 3, 2 and 1) obtained at least 1 hour apart, and then adding a 20% buffer to this value (see also Lambardi et al. 2008). A minimum individual speed threshold of 4 km/h was anyway used.

The turtle reconstructed movements were divided into four successive phases: i) inter-nesting ii) post-reproductive migration, iii) stay at the foraging ground and iv) pre-breeding migration. For pre- and post-breeding migration the Straightness Index (Batschelet 1981) was calculated as the ratio between the distance from the starting point to the final destination and the actual path length covered to reach the goal.

2.4. Home range analysis

Individual turtles' home ranges were calculated during their stay at neritic foraging grounds upon completing the post-nesting migration. The density of the utilization distribution (UD) of

turtle locations was estimated using the fixed kernel technique (Worton 1989). The 95% volume contour (K95%) was used as home range polygon. Following Kie (2013), the *ad hoc* bandwidth or smoothing parameter (*h ad hoc*) was independently selected for each individual by sequentially reducing the reference bandwidth (HREF, *i.e.* the optimal bandwidth under the assumption of bivariate normality) in 0.10 increments and choosing the smallest increment of HREF that: 1) resulted in a contiguous K95% polygon, and 2) contained no lacuna within K95%. When the estimated home range was fragmented at HREF we set *h ad hoc* = HREF.

Individual core areas were identified by applying the Area Independent Method developed by Seaman and Powell (1990). The method divides the home range in areas of high and low use using an objective criterion, and is based on a graphical representation of the home range area in relation to its use (UD volume contour). In this way it is possible to identify the dividing point between high- and low-use areas, as the point where the plot is maximally distant from a straight line of slope +/-1, that represents a distribution of random use. We performed the analysis considering steps = 5%. In all our turtles the point of maximum distance was reached at a value close to 80% volume contour and so we defined the core area in this way.

For each turtle, the kernel analysis was calculated on the whole data set and separately on the locations obtained during the summer and winter period. The separation between the two periods was clearly identifiable from the presence of a directed movement leading the turtles to shift between distinct core areas (see Results for details).

Calculations were made with the *adehabitatHR* package in R 3.2.2 (R Core Team 2015).

2.5. Behavioural Change Point Analysis

To obtain insights on the turtle spatial behaviour, the inter-nesting, post-nesting and pre-breeding movements have been subjected to an in-depth elaboration through a Behavioural

Change Point Analysis (BCPA; Gurarie et al. 2009). This method - recently applied to the study of sea turtle movements (Patel et al. 2015) - measures the tendency of a movement to persist in a given direction (persistent velocity), aiming at identifying points ('Change Points', CPs) where a behavioural change in the animal movement took place (Gurarie et al. 2009). For our analysis, we used a 'flat' method, with a windows size of 20 successive fixes and considering all the change points determined by BCPA (cluster width 0), identified by at least 6 windows. Calculations were made with the *bcpa* package 1.1 in R 3.2.2.

2.6. Ocean current analysis

Data on ocean currents were obtained from the Mediterranean Forecasting System (<http://marine.copernicus.eu/>; Pinardi et al. 2003; Tonani et al. 2009). They are based on a state-of-the-art three-dimensional model (Oddo et al. 2009), and have been already employed in previous turtle studies in the Mediterranean (Hays et al. 2013). Daily mean data at the minimum available depth (i.e., -1.47 m; Clementi et al. 2015) were used, given that loggerhead turtles are known to travel near the surface (Hochscheid et al. 2014). The model has an horizontal spatial resolution of $1/16^\circ$ (around 6-7 km).

Following previous studies (Gaspar et al. 2006; Galli et al. 2012), filtered locations were re-sampled with a sampling period of 4 hours, and a track vector was computed between successive resampled positions, representing the ground-related velocity of the tracked turtle averaged over the 4-hr time interval. At each resampled position, a surface current vector was then computed using the u and v components estimated by the ocean circulation model at the point closest to the turtle interpolated position. Finally, we calculated the swimming vector of the turtle over the 4-hr time interval as the vector difference between the other two vectors (Gaspar et al. 2006), which represents the actual swimming movement of the turtle.

3. Results

With the exception of turtle *Esperia* (see below, and Tab. 1), all turtles were tracked for more than 300 days (range: 313-1523 days, mean $774,8 \pm 445,6$ SD), and this allowed to monitor three turtles (Kalabria, Lacina and Ellenia) for the entire remigration interval of 2/3 years between successive breeding seasons.

3.1. Inter-nesting movements

Four females were tracked during 1-4 inter-nesting periods, for a total of 10 inter-nesting movements (Tab. 2). Successive nesting events of all tracked turtles occurred along the study area coast, although Ellenia nested 25 km north of it in 2014. Successive egg-layings for the single females were separated by 0.7-26.5 km (median 9.0 km). During inter-nesting, all turtles moved away from the nesting area, usually embarking in long-distance loops occurring mostly in oceanic waters (Fig. 2), which usually extended to >100 km away from the coast (median maximum distance from nesting location: 145.5 km, Tab. 2), and for an overall trip length ranging from 279 to 892 km (median 496 km). In the three turtles monitored during successive inter-nesting periods (Kalabria, Lacinia, and Ellenia), the first loop was always farther away than the successive ones (Tab. 2), that were shorter and more meandering (Fig. 2). The turtles were consistent in the distance travelled, i.e. the animals moving farther away from the nesting area during the first movement behaved in the same way also in the successive inter-nesting periods (Tab. 2).

The long-distance loops were all done in areas where only weak currents (0.08-0.14 m/s) were present, and no major changes in turtle movement speeds along the route were evident, although turtles *Isodia* and *Lacinia* (both in 2010 and 2012) displayed a tendency to move quicker during the second phase of the loop, when returning towards the Calabrian coast. BCPA indeed revealed CPs along 8 out of 10 inter-nesting routes, with a CP falling around half of the journey in 6 cases (Fig. 2).

3.2. Post-nesting migrations

After completing the nesting cycle, all turtles migrated towards the continental shelf offshore Tunisia (Fig. 3), with the only exception of *Zeffiria* (Online Resource ESM Fig. 1), who remained in the oceanic waters East of Malta Island for the tracking period (313 days, although with a 6-months gap in between). The initial behaviour of turtle *Eracleia* was enigmatic: she left the Calabrian coast immediately after PTT attachment, reaching the coastal waters of south-eastern Sicily after 10 days, where she remained for further 11 days, before eventually moving towards the Tunisian shelf (Fig. 3). The other turtles initially moved through a rather narrow corridor oriented towards SW (Fig. 3), that led them to quickly reach the waters around Malta in 4-7 days (mean track directions range before reaching the latitude of Malta: $198-219^\circ$, $n = 9$ migrations). In most cases turtles passed Malta from the southeast, with only turtle *Lacinia* in 2012 hugging the northern coasts of Malta and Gozo Islands before turning southwest again. South of Malta the routes diverged, with most turtles ($n = 7$ migrations) continuing to move southwest, and turtle *Kalabria* following in both years a more western route. Straightness indexes of the various routes ranged between 0.50 and 0.83.

The area crossed during the post-nesting migrations is characterised by a general lack of strong currents, with the only exception of the persistent Atlantic-Ionian stream (Poulain et al.

2012) that flows south-easterly between southern Sicily and Malta Island in the summer period (Fig. 4). The turtles thus crossed the main current roughly at right angle, but current intensity was moderate (around 0.3 m/s) and its actual effect on the turtle movement was limited (Online Resource ESM Fig. 2). BCPA identified a number of change points along the post-nesting routes (mean 3.0 per route), but no overall spatial and/or temporal pattern was evident (Fig. 3).

The turtles' final destinations were distinct and circumscribed sites over the Tunisian shelf (Fig. 5), where the turtles were then localised for the successive months while staying at their foraging sites (see below). The three turtles that were tracked during successive seasons (Lacinia and Kalabria in 2010 and 2012, Ellenia in 2011 and 2014), returned to the very same site, following similar (Lacinia) or almost coincident (Kalabria and Ellenia) routes.

3.3. Stay at the foraging grounds

The home ranges of the five turtles tracked during their stay at the foraging grounds are shown in Fig. 5 (details can be found in Online Resource ESM Tab. 1). Turtle Esperia is not included in this analysis since five days after she reached the Tunisian coast (entering the Boughrara Gulf) she was localised on the coast (close to the town of Guellala, Tunisia), with satellite-relayed sensor data indicating that the transmitter was out of the water. We conclude that the transmitter likely detached from the turtle or that the turtle itself was captured.

The remaining turtles occupied sites that, although not strictly coastal, were in the neritic environment (median depth of the recorded locations in the different turtles ranging between 5 and 81 m). With the exception of Eracleia, the turtles occupied clearly distinct sites during the summer and winter months, moving to the winter site between November and December and then returning to the summer site in April, in both cases making quick directed movements between the two areas, that were 50-100 km away (Fig. 5). The three turtles that were tracked for

multiple years shuttled between the very same sites, up to a total of four times in Ellenia. The 95% Kernel seasonal home ranges were partly overlapping in turtles Kalabria and Lacinia, but were totally distinct in turtles Isodia and Ellenia, while seasonal core areas (80% Kernel) were separated in all turtles. The winter core areas of the four turtles were largely overlapping, being all located East of Kerkennah Island. The size of the winter home range and core area was larger than the summer ones in all turtles (median core area size: 498 km² in winter, 258 km² in summer; Tab. A1).

Thanks to the long tracking period, a high fidelity to the individual seasonal sites was demonstrated, with turtles returning to the very same area in successive years (mean proportion of individual home range overlap: summer 0.72±0.16 DS, winter 0.64±0.26; Online Resource ESM Tab.2, ESM Fig. 3A, 3B). While in summer (Online Resource ESM Fig. 3A) there was no overlap among different turtles, in winter (Online Resource ESM Fig. 3B), conversely, the individuals tended to cluster East of Kerkennah Island (mean proportion of inter-individual home range overlap: 0.28±0.30).

3.4. Pre-breeding migrations

Three turtles were tracked for long enough to reconstruct their migration back to the nesting sites, after a two- (turtles Lacinia and Kalabria) or three- (turtle Ellenia) years stay at their foraging sites. Differently from the post-nesting migrations, the routes of the three turtles were rather dissimilar (Fig. 6). Turtle Kalabria started her migration on 21 May 2012 and initially took a very straight course to the northeast (*i.e.*, keeping an heading that would have led her directly to the nesting area). She then circumnavigated the southeastern part of Sicily before reaching the southern Calabrian coast with a fairly direct route. She arrived in the breeding area after 29 days of migration covering 694 km (straightness index: 0.82), nesting a few hours later at a site that

was only 3 km away from the site where she made her last egg-laying in 2010. Turtle Lacinia left the foraging site on 19 May 2012, but compared to Calabria followed a most different route, taking an easterly course that led her to cross the southern Ionian Sea well south of the Italian Peninsula. Only after 20 days of travel, when she was around 60 km southwest of the westernmost Greek islands (Cephalonia and Zakynthos Is.), did she change her course towards the northwest, reaching the northern Calabrian coast after further eight days. She then hugged the coast for seven days and then nested on 22 June, 6 km south of her last nesting site in 2010. She covered a total of 1643 km over 35 days with a route straightness index of 0.37. Turtle Ellenia left her feeding area at the end of May 2014, initially moving eastward and then shifting to a north-northeast course after about ten days, reaching the Calabrian coast a week later (total route length 685 km; straightness index: 0.69). She then moved north for about 25 km to make her first egg-laying on the following night (17 June) at a location that was 5 km away from her last nesting site in 2011.

4. Discussion

The findings obtained in this study provide relevant information on a number of aspects of the spatial behaviour of Mediterranean loggerhead turtles.

4.1. General migratory strategy

First, our results offer a complete documentation of the migration pattern of the loggerhead rookery of the Ionian Calabrian coast, that constitutes the main nesting ground in Italy (Mingozzi et al. 2007). This population is known to be genetically distinct from the other loggerhead rookeries in the basin (Garofalo et al. 2013), contributing significantly to the overall Mediterranean mtDNA haplotype diversity (Garofalo et al. 2009), and is thought to have

originated from a foundation event subsequent to those that gave rise to the other Mediterranean rookeries (Clusa et al. 2013). Given that the rookery size is conservatively estimated around 20-25 nesting females (seasons 2013 and 2014; Mingozzi unpubl data), our sample of seven females represents a substantial fraction of the population. Information on the spatial behaviour of tracked turtles is therefore particularly valuable also for conservation purposes.

The overall migratory strategy outlined is fully in accordance with that known in most adult loggerheads tracked so far: a quick movement away from the breeding site directed towards a specific foraging area in the neritic environment (type A pattern, Godley et al. 2008). The routes of different turtles displayed an overall similarity, all being initially clustered in a sort of migratory corridor running from Calabria to the southwest of Malta (Fig. 3). The successive post-nesting tracks of the same turtle were strikingly similar, showing an individual fidelity to a given migratory route, in full accordance with previous findings in loggerheads (Broderick et al. 2007; Hart et al. 2014, 2015; Tucker et al. 2014) and in other turtle species (Broderick et al. 2007; Hawkes et al. 2012). Exceptions to this pattern are represented by turtle Zeffiria, that frequented pelagic waters throughout the tracking period (type B pattern, Godley et al. 2008), and by turtle Eracleia, which, before moving towards the Tunisian shelf, spent 11 days close to the South-eastern coast of Sicily. It is possible that she nested during this period in this area that is about 155 km from the Calabrian coast (a distance shorter than the maximum distance between successive nests reported for a single turtle within a season; e.g., Hart et al. 2013) - but we have no direct indications corroborating this hypothesis. The Sicilian area is not known as a main turtle nesting site, although sporadic activity has been signalled in some beaches close to the area visited by turtle Eracleia (Insacco et al. 2011).

The fact that all post-nesting females headed south or southwest highlights a major difference with the migratory pattern known for other Mediterranean rookeries (e.g. Zakynthos, Crete and Cyprus) where two or more migratory directions are usually evident (Schofield et al. 2013a;

Patel et al. 2015; Snape et al. 2016). It has been speculated that the migratory directional choices of adults reflect the current pattern experienced by hatchlings during their dispersal (Hays et al. 2010a), but we currently have no information on hatchling dispersal for the Calabrian population. The main destination of tracked turtles, i.e., the Tunisian continental shelf, is one of the largest neritic areas of the basin and, as such, is known to represent a main foraging sites for Mediterranean turtles, used by both juveniles (Casale et al. 2012) and adults (Broderick et al. 2007; Zbinden et al. 2008; Schofield et al. 2013a; Snape et al. 2016), including males (Schofield et al. 2013a; Casale et al. 2013). An exception to this pattern is turtle *Zeffiria*, that frequented pelagic waters throughout the tracking period (type B pattern, Godley et al. 2008). These findings nicely complement the existing data on the migrations of Mediterranean loggerheads (reviewed by Luschi and Casale 2014) and help to delineate an overall picture of the phenomenon, since the available information is still quite fragmentary and biased towards the major rookeries in Greece (Zbinden et al. 2008; Schofield et al. 2010c; Patel et al. 2015) and Cyprus (Broderick et al. 2007; Snape et al. 2016).

4.2. Spatial behaviour throughout the inter-reproductive cycle

Thanks to the very long duration of the tracking (up to >1500 days), we have also been able to record the behaviour of three turtles during the complete inter-reproductive cycle of 2 or 3 years, comprising the inter-nesting movements, the shuttling migrations between individually-specific nesting and foraging sites, and the short-scale movements at the foraging grounds. The presence of shuttling migrations in loggerheads and other hard-shelled turtles has so far been supported by multiple recoveries or resightings at a foraging site of females tagged while nesting (Balazs 1983, Limpus et al. 1992), and by a mechanistic model of breeding periodicity (Hays et al. 2014). The present findings provide a complete and clear documentation of the phenomenon,

unequivocally showing how loggerhead females faithfully return to individually-specific nesting and foraging sites in subsequent years. A similar fidelity to foraging sites has been demonstrated in long-term satellite tracking studies on Brazilian loggerhead females (Broderick et al. 2007; Marcovaldi et al. 2010, Hart et al. 2014, 2015), on Mediterranean males (Casale et al. 2012; Schofield et al. 2010a), and in hawksbill females (Hawkes et al. 2012). In the Brazilian study, a spatial pattern fully corresponding to the present one was shown, with individual turtles faithfully returning to the same neritic foraging site in two successive seasons migrating along the coast (Marcovaldi et al. 2010). Fidelity to the same route during successive post-nesting migrations was also shown in three turtles, in accordance with previous findings (Broderick et al. 2007; Hart et al. 2014, 2015).

The reconstruction of the pre-nesting migrations of three females provides valuable information on this very poorly studied phase of the turtle life cycle (Godley et al. 2008). The three turtles followed different routes to get back to their nesting ground, that were more (turtle Ellenia) or less (turtle Kalabria, but above all turtle Lacinia) oriented towards the destination (Fig. 6). We have no explanation for such variable and quite enigmatic behaviours. The few other pre-nesting migrations tracked in loggerhead females (Zbinden et al. 2008; Marcovaldi et al. 2010) and males (Hays et al. 2010b; Schofield et al. 2010a, Casale et al. 2013), as well as in other species (Hawkes et al. 2012; Marcovaldi et al. 2012) are all well oriented towards the nesting/breeding area and do not show such detours. One possibility is that the turtle was initially heading to a mating site, but it seems unlikely that some Calabrian females have to make such long detours to find males. Satellite findings cannot provide any clue as to where mating occurred, so we cannot establish this for Lacinia as well as for the other two females, although some indications can be obtained from the temporal pattern of the turtle arrival to the breeding/nesting area. Since the three turtles reached the Calabrian coast a few days (Lacinia) or hours (Kalabria and Ellenia) before their first egg-laying, it can be excluded that they mated in

the nesting area (as frequently happens; Miller 1997), at least to fertilise the first clutch. At Zakynthos Is., mating occurs close to the nesting beach about 3 months before the nesting season begins, with females arriving even before that (Schofield et al. 2013b). It is therefore likely that our turtles had mated at the foraging sites before starting their migration, or perhaps en route (e.g., Lacinia), in line with the long interval between mating and nesting recorded for Zakynthos females (Schofield et al. 2013b). Such a mating activity away from breeding sites, which is fundamental in assuring gene flow between different rookeries (Bowen and Karl 2007), may be an effect of a very low male density in the nesting area that would force females to search for males elsewhere. Actually, only two adult males have been hospitalized in the last 10 years at a turtle rescue centre close to the nesting beaches (CRTM, Brancaleone; F. Armonio pers. comm.).

4.3. Inter-nesting movements

The 10 inter-nesting routes reconstructed for four turtles revealed the unusual behaviour of making extended loops in the oceanic environment, a pattern more typical of pelagic-dwelling species (e.g. Keinath and Musick 1993; Plotkin et al. 1995; Fossette et al. 2007). Loggerheads typically remain in the vicinity of the nesting beach between nesting events, although a few cases of large-scale oceanic movements are known (Blumenthal et al. 2006; Rees et al. 2010), as well as of forays outside the breeding area (Schofield et al. 2010b). It can be hypothesised that such long oceanic movements were induced by the need of replenishing the females' food stores after an egg-laying: given the limited availability of neritic areas offshore the nesting region, due to the small continental shelf of the Ionian Calabrian coast, females were likely prompted to move offshore to forage. Epipelagic feeding in oceanic areas has recently been recorded in some post-nesting loggerheads (Hatase et al. 2002, Hawkes et al. 2012).

4.4. Behaviour at the foraging grounds

The detailed reconstruction of the small-scale movements at the foraging grounds in four turtles revealed the presence of inter-foraging migrations between two distinct areas during the year. Turtles moved towards the wintering areas between October and December, while they all returned to the summer sites in the very same period (first two weeks of April). Individual summer areas were located along the Tunisian coast and separated, whereas winter sites were all clustered (Fig. 5). Seasonal movements between widely separated foraging areas are well known in loggerheads (e.g. Zbinden et al. 2008; Griffin et al. 2013), while short-distance inter-foraging migrations have been documented only in females foraging offshore Libya moving for a few tens of km to deeper waters in winter (Broderick et al. 2007) and in males tracked in the very same area as our turtles (Casale et al. 2013). Our findings additionally show how individual turtles shuttled between these two specific sites in successive years, displaying an high fidelity to both sites. It may appear surprising that turtles are faithful to two such adjacent sites: it is likely that they provide seasonally variable foraging opportunities to turtles and/or are characterised by specific environmental characteristics. For instance, water temperature may play a role in this shift, given that loggerheads have been shown to select a specific range of temperatures (Coles and Musick 2000; Hawkes et al. 2011). On this connection, it is worth recalling that turtle *Eracleia* conversely remained in the same, more southern area throughout the year, as is known in other cases of long-term tracking (Papi et al. 1997; Broderick et al. 2007; Snape et al. 2016). This variation can be attributed to the known behavioural plasticity of loggerheads, which can follow different strategies during the foraging period, including that of moving along large stretches of coast without fixing to a site or another (Zbinden et al. 2008; Casale et al. 2013).

One of the main finding of this study is the recorded strong fidelity of individual turtles to specific foraging sites in successive years, that was suggested, but not analysed in depth, in

previous Mediterranean studies (Zbinden et al. 2008, Casale et al. 2013). Furthermore, a different seasonal distribution pattern was observed among the individual turtles, which remained in non-overlapping areas in summer while tended to aggregate in winter. To our knowledge, this is the first time that such a pattern is revealed. We have no direct hints to explain this behaviour, and we may only hypothesise that a different distribution of food resources during the year may account for the observed pattern.

The absolute values of home range size found in this study are broadly comparable to those previously estimated (Broderick et al. 2007; Zbinden et al. 2008; Casale et al. 2013) although comparison with other studies is difficult because home range estimations have been done using different methods (Minimum Convex Polygon or Kernel Methods with different bandwidth). Home range size varied largely among individual turtles (Tab. A1), with two females (Lacinia and Kalabria) occupying wider areas than the other two. Such an inter-individual variation in home range size has been observed also in turtles foraging in the Adriatic Sea and along the Tunisian shelf (Zbinden et al. 2008; Casale et al. 2013; Schofield et al. 2010a). In some of these studies, the winter area was smaller than the summer one (Broderick et al. 2007; Zbinden et al. 2008), while an opposite pattern was observed in our case, with all turtles frequenting a larger area during the colder months. Once again, loggerheads reveal a plasticity in their behaviour, apparently adapting their habitat choice to different micro-geographic areas, likely in relation to differing environmental factors.

5. Conclusions

To sum up, this study provides a complete documentation of the spatial behaviour of Mediterranean loggerheads during an entire reproductive cycle. In this way, relevant information on this marginal and genetically distinct population was obtained: in particular, the use of a

migratory corridor and the strong fidelity to specific foraging sites, further highlight the importance of the oceanic zones of central Mediterranean and of the Tunisian shelf for the conservation of Mediterranean loggerheads.

Author contributions

T. Mingozi and P. Luschi designed the experiments, G. Cerritelli, R. Mencacci and D. Giunchi analysed the data. All the authors edited and contributed to the article and approved the final manuscript.

Compliance with ethical standards

All authors have examined and agree on the manuscript, have agreed to be listed and contributed to the research reported. The Authors declare that they have no conflict of interest. The study complies with Institutional, national and international ethics guidelines concerning the use of animals in research and/or the sampling of endangered species. None of the procedures used in the study met the criteria to define them "experiments" as defined in Article 2 of the EEC Directive 86/609/EEC regarding the protection of animals used for experimental and other scientific purposes.

Acknowledgements

This research was partially supported with funding from Regione Calabria, Dipartimento Politiche dell'Ambiente (monetary agreements with University of Calabria n. 4038 of 16 December 2009 and n. 6811 of 18 April 2011).

Transmitter deployments were made thanks to the authorizations (DPN-2008-0008603 of 2 April 2008; DPN-2010-0001461 of 28 January 2010; PNM-II 0028447 of 18 October 2012) of the "MATTM" (Italian Ministry of Environment, General Direction for Nature Protection).

The authors are grateful to the collaborators, students and volunteers thanks to whose efforts on the fieldwork the transmitter deployments were achieved, in particular Salvatore Urso and Gianni Parise, Maria Concetta Denaro, Teresa Malito, Carmela Mancuso, Animo Fragiacomò, Simona Fabiano, Igor Gambaro, and Pierpaolo Storino.

We would also like to thank Prof Alessandro Massolo (Calgary, CA) and Dr Paolo Casale (Rome, I) for their useful comments on an early version of the MS. Finally, a special thanks is due to Dr G. Hays for reviewed comments that significantly improved the overall quality of the paper.

References

- Balazs, G.H., 1983. Recovery records of adult green turtles observed or originally tagged at French Frigate Shoals, Northwestern Hawaiian Islands. NOAA Technical Memorandum, NMFS-SWFC-36, 1-42.
- Batschelet, E., 1981. Circular statistics in biology, Academic Press, New York.
- Blumenthal, J.M., Solomon, J.M., Bell, C.D., Austin, T.J., Ebanks-Petrie, G., Coyne, M., Broderick, A.C., Godley, B.J., 2006. Satellite tracking highlights the need for international cooperation in marine turtle management. *Endanger. Species Res.* 2, 51-61.

- Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* 11, 63-77.
- Bowen, B.W., Karl, S.A., 2007. Population genetics and phylogeography of sea turtles. *Mol. Ecol.* 16, 4886-4907.
- Broderick, A.C., Coyne, M., Fuller, W.J., Glen, F., Godley, B.J., 2007. Fidelity and overwintering of sea turtles. *Proc. R. Soc. B* 274, 1533-1538.
- Casale, P., Margaritoulis, D., 2010. Sea turtles in the Mediterranean: Distribution, threats and conservation priorities, IUCN, Gland, Switzerland.
- Casale, P., Affronte, M., Scaravelli, D., Lazar, B., Vallini, C., Luschi, P., 2012. Foraging grounds, movement patterns and habitat connectivity of juvenile loggerhead turtles (*Caretta caretta*) tracked from the Adriatic Sea. *Mar. Biol.* 159, 1527-1535.
- Casale, P., Freggi, D., Cinà, A., Rocco, M., 2013. Spatio-temporal distribution and migration of adult male loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea: further evidence of the importance of neritic habitats off North Africa. *Mar. Biol.* 160, 703-718.
- Clementi, E., Grandi, A., Di Pietro, P., Pistoia, J., Delrosso, D., Cossarini, G., 2016. Quality information document for Mediterranean Sea physical analysis and forecasting products. EU Copernicus Marine Service, CMEMS-MED-QUID-006-001-V2.
- Clusa, M., Carreras, C., Pascual, M., Gaughran, S.G., Piovano, S., Giacoma, C., Fernandez, G., Levy, Y., Tomas, J., Raga, J.A., Maffucci, F., Hochscheid, S., Aguilar, A., Cardona, L., 2013. Mitochondrial DNA reveals Pleistocenic colonisation of the Mediterranean by loggerhead turtles (*Caretta caretta*). *Mar. Biol.* 161, 509-519.
- Coles, W.C., Musick, J.A., 2000. Satellite sea surface temperature analysis and correlation with sea turtle distribution off North Carolina. *Copeia* 2000, 551-554.

- Coyne, M.S., Godley, B.J., 2005. Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Mar. Ecol. Prog. Ser.* 301, 1-7.
- Eckert, C.G., Samis, K.E., Lougheed, S.C., 2008. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol. Ecol.* 17, 1170-1188.
- Forman, R.T.T., Godron, M., 1986. *Landscape ecology*, John Wiley & Sons, New York.
- Fossette, S., Ferraroli, S., Tanaka, H., Ropert-Courbet, Y., Arai, N., Sato, K., Naito, Y., Le Maho, Y., Georges, J.Y., 2007. Dispersal and dive patterns in gravid leatherback turtles during the nesting season in French Guiana. *Mar. Ecol. Prog. Ser.* 338, 223-247.
- Galli, S., Gaspar, P., Fossette, S., Calmettes, B., Hays, G.C., Lutjeharms, J.R.E., Luschi, P., 2012. Orientation of migrating leatherback turtles in relation to ocean currents. *Anim. Behav.* 84, 1491-1500.
- Garofalo, L., Mingozi, T., Micò, A., Novelletto, A., 2009. Loggerhead turtle (*Caretta caretta*) matriline in the Mediterranean: further evidence of genetic diversity and connectivity. *Mar. Biol.* 156, 2085-2095.
- Garofalo, L., Mastrogiacomo, A., Casale, P., Carlini, R., Eleni, C., Freggi, D., Gelli, D., Knittweis, L., Mifsud, C., Mingozi, T., Novarini, N., Scaravelli, D., Scillitani, G., Oliviero, M., Novelletto, A., 2013. Genetic characterization of central Mediterranean stocks of the loggerhead turtle (*Caretta caretta*) using mitochondrial and nuclear markers, and conservation implications. *Aquat. Conserv.* 23, 868-884.
- Gaspar, P., George, J.C., Fossette, S., Lenoble, A., Ferraroli, S., Le Maho, Y., 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc. R. Soc. B* 273, 2697-2702.

- Godley, B.J., Blumenthal, J.M., Broderick, A.C., Coyne, M., Godfrey, M.H., Hawkes, L.A., Witt, M.J., 2008. Satellite tracking of sea turtles: Where have we been and where do we go next? *Endanger. Species Res.* 4, 3-22.
- Griffin, D.B., Murphy, S.R., Frick, M.G., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, G.M., Godfrey, M.H., Godley, B.J., Hawkes, L.A., Murphy, T.M., Williams, K.L., Witt, M.J., 2013. Foraging habitats and migration corridors utilized by a recovering subpopulation of adult female loggerhead sea turtles: implications for conservation. *Mar. Biol.* 160, 3071-3086.
- Gurarie, E., Andrews, R.D., Laidre, K.L., 2009. A novel method for identifying behavioural changes in animal movement data. *Ecol. Lett.* 12, 395-408.
- Hansson, L.A., Åkesson, S., 2014. *Animal movement across scales*, Oxford University Press, Oxford, UK.
- Hart, K.M., Hyrenbach, K.D., 2009. Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endanger. Species Res.* 10, 9-20.
- Hart, K.M., Lamont, M.M., Sartain, A.R., Fujisaki, I., Stephens, B.S., 2013. Movements and habitat-use of loggerhead sea turtles in the northern Gulf of Mexico during the reproductive period. *Plos One* 8 (7), e66921.
- Hart, K.M., Lamont, M.M., Sartain, A.R., Fujisaki, I., 2014. Migration, foraging, and residency patterns for Northern Gulf loggerheads: implications of local threats and international movements. *PLoS One* 9 (7), e103453.
- Hart, K.M., Sartain, A.R., Fujisaki, I., 2015. Bahamas connection: residence areas selected by breeding female loggerheads tagged in Dry Tortugas National Park, USA. *Anim. Biotelem.* 3, 3.
- Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N., Fujiwara, T., 2002. Size-related differences in feeding habitat use of adult female loggerheads *Caretta*

- caretta* around Japan determined by stable isotope analyses and satellite telemetry. Mar. Ecol. Prog. Ser. 233, 273-281.
- Hawkes, L.A., Witt, M.J., Broderick, A.C., Coker, J.W., Coyne, M., Dodd, C.K., Frick, M.G., Godfrey, M.H., Griffin, D.B., Murphy, S.R., Murphy, T.M., Williams, K.L., Godley, B.J., 2011. Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Divers. Distrib. 17, 624-640.
- Hawkes, L.A., Tomas, J., Revuelta, O., Leon, Y.M., Blumenthal, J.M., Broderick, A.C., Fish, M., Raga, J.A., Witt, M.J., Godley, B.J., 2012. Migratory patterns in hawksbill turtles described by satellite tracking. Mar. Ecol. Prog. Ser. 461, 223-232.
- Hays, G.C., Fossette, S., Katselidis, K.A., Mariani, P., Schofield, G., 2010a. Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. J. R. Soc. Interface 7, 1319-1327.
- Hays, G.C., Fossette, S., Katselidis, K.A., Schofield, G., Gravenor, M.B., 2010b. Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. Conserv. Biol. 24, 1636-1643.
- Hays, G.C., Christensen, A., Fossette, S., Schofield, G., Talbot, J., Mariani, P., 2013. Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. Ecol. Lett. 17, 137-143.
- Hays, G.C., Mazaris, A.D., Schofield, G., 2014. Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. Frontiers in Marine Science 1, art. 43.
- Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen, B.W., Caley, M.J., Costa, D.P., Eguiluz, V.M., Fossette, S., Friedlaender, A.S., Gales, N., Gleiss, A.C., Gunn, J., Harcourt, R., Hazen, E.L., Heithaus, M.R., Heupel, M., Holland, K., Horning, M., Jonsen, I., Kooyman, G.L., Lowe, C.G., Madsen, P.T., Marsh, H., Philips, R.A., Righton, D., Ropert-Coudert, Y., Sato, K., Shaffer, S.A., Simpfendorfer, C.A.,

- Sims, D.W., Skomal, G., Takahashi, A., Trathan, P.N., Wikelski, M., Womble, J.N., Thums, M., 2016. Key questions in marine megafauna movement ecology. *TREE* 31, 462-475.
- Hochscheid, S., 2014. Why we mind sea turtles' underwater business: A review on the study of diving behavior. *J. Exp. Mar. Biol. Ecol.* 450, 118-136.
- Insacco, G., Barlotta, A., Bentivegna, F., Scaravelli, D., Spadola, F., Hochscheid, S., 2011. Sicily 2010 nest season: bad weather and good news. In: 4th Mediterranean Conference on Marine Turtles, Naples 7-11 Sept. 2011, 78 pp.
- Keinath, J.A., Musick, J.A., 1993. Movements and diving behavior of a leatherback turtle, *Dermochelys coriacea*. *Copeia* 1993, 1010-1017.
- Kernohan, B.J., Gitzen, R.A., Millspaugh, J.J., 2001. Analysis of animal space use and movements. In: Millspaugh, J.J., Marzluff, J.M. (Eds.), *Radio tracking animal populations*, Academic Press, pp. 125-166.
- Lambardi, P., Lutjeharms, J.R.E., Mencacci, R., Hays, G.C., Luschi, P., 2008. Influence of ocean currents on long-distance movement of leatherback sea turtles in the Southwest Indian Ocean. *Mar. Ecol. Prog. Ser.* 353, 289-301.
- Lesica, P., Allendorf, F.W., 1995. When are peripheral populations valuable for conservation? *Conserv. Biol.* 9, 753-760.
- Limpus, C.J., Miller, J.D., Parmenter, C.J., Reimer, D., McLachlan, N., Webb, R., 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildl. Res.* 19, 347-358.
- Luschi, P., Casale, P., 2014. Movement patterns of marine turtles in the Mediterranean Sea: a review. *Ital. J. Zool.* 81, 478-495.
- Mansfield, K.L., Wyneken, J., Porter, W.P., Luo, J., 2014. First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. *Proc. R. Soc. B* 281, 20133039.

- Marcovaldi, M.A., Lopez, G.G., Soares, L.S., Lima, E.H.S., Thomé, J.C.A., Almeida, A.P., 2010. Satellite-tracking of female loggerhead turtles highlights fidelity behavior in northeastern Brazil. *Endanger. Species Res.* 12, 263-272.
- Marcovaldi, M.A., Lopez, G.G., Soares, L.S., Lopez-Mendilaharsu, M., 2012. Satellite tracking of hawksbill turtles *Eretmochelys imbricata* nesting in northern Bahia, Brazil: turtle movements and foraging destinations. *Endanger. Species Res.* 17, 123-132.
- Miller, J.D., 1997. Reproduction in sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*, CRC Press, Boca Raton, pp. 51-82.
- Mills, L.S., 2013. *Conservation of Wildlife Populations: Demography, Genetics, and Management*, John Wiley & Sons, Ltd, Oxford, UK.
- Mingozzi, T., Masciari, G., Paolillo, G., Pisani, B., Russo, M., Massolo, A., 2007. Discovery of a regular nesting area of loggerhead turtle *Caretta caretta* in southern Italy: a new perspective for national conservation. *Biodivers. Conserv.* 16, 3519-3541.
- Musick, J.A., Limpus, C.J., 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*, CRC Press, Boca Raton, pp. 137-164.
- Oddo, P., Adani, M., Pinardi, N., Fratianni, C., Tonani, M., Pettenuzzo, D., 2009. A nested Atlantic-Mediterranean Sea general circulation model for operational forecasting. *Ocean Sci.* 5, 461-473.
- Palumbi, S.R., 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annu. Rev. Env. Resour.* 29, 31-68.
- Papi, F., Luschi, P., Crosio, E., Hughes, G.R., 1997. Satellite tracking experiments on the navigational ability and migratory behaviour of the loggerhead turtle *Caretta caretta*. *Mar. Biol.* 129, 215-220.

- Patel, S.H., Panagapoulou, A., Morreale, S.J., Kilham, S.S., Karakassis, I., Riggall, T.E., Margaritoulis, D., Spotila, J.R., 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.
- Piersma, T., Baker, A.J., 2000. Life history characteristics and conservation of migratory shorebirds. In: Gosling, L.M., Sutherland, W.J. (Eds.), *Behaviour and Conservation*, Cambridge University Press, Cambridge, UK, pp. 105-124.
- Pinardi, N., Allen, I., Demirov, E., De Mey, P., Korres, G., Lascaratos, A., Le Traon, P.-Y., Maillard, C., Manzella, G., Tziavos, C., 2003. The Mediterranean ocean forecasting system: first phase of implementation (1998-2001). *Ann. Geophys.* 21, 3-20.
- Plotkin, P.T., Byles, R.A., Rostal, D.C., Owens, D.W., 1995. Independent versus socially facilitated oceanic migrations of the olive ridley, *Lepidochelys olivacea*. *Mar. Biol.* 122, 137-143.
- Plotkin, P.T., 2003. Adult migrations and habitat use. In: Lutz, P.L., Musick, J.A., Wyneken, J. (Eds.), *The Biology of Sea Turtles*, Vol. II, CRC Press, Boca Raton, FL, USA, pp. 225-241.
- Poulain, P.-M., Menna, M., Mauri, E., 2012. Surface geostrophic circulation of the Mediterranean Sea derived from drifter and satellite altimeter data. *J. Phys. Oceanogr.* 42, 973-990.
- R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, <https://www.r-project.org/>
- Rees, A.F., Al Saady, S., Broderick, A.C., Coyne, M.S., Papathanasopoulou, N., Godley, B.J., 2010. Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*. *Mar. Ecol. Prog. Ser.* 418, 201-212.

- Reynolds, J.D., Jennings, S., 2000. The role of animal behaviour in marine conservation. In: Gosling, L.M., Sutherland, J.M. (Eds.), *Behaviour and Conservation*, Cambridge University Press, Cambridge, UK, pp. 238-257.
- Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A., Hays, G.C., 2010a. Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Divers. Distrib.* 16, 840-853.
- Schofield, G., Hobson, V.J., Lilley, M.K.S., Katselidis, K.A., Bishop, C.M., Brown, P., Hays, G.C., 2010b. Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. *Biol. Conserv.* 143, 722-730
- Schofield, G., Lilley, M.K.S., Bishop, C.M., Brown, P., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2010c. Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. *Endanger. Species Res.* 10, 191-202.
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, K.A., Koutsoubas, D., Lilley, M.K.S., Luckman, A., Pantis, J.D., Karagouni, A.D., Hays, G.C., 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.
- Schofield, G., Scott, R., Dimadi, A., Fossette, S., Katselidis, K.A., Koutsoubas, D., Lilley, F.E.M., Pantis, J.D., Karagouni, A.D., Hays, G.C., 2013b. Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. *Biol. Conserv.* 161, 101-109.
- Seaman, D.E., Powell, R.A., 1990. Identifying patterns and intensity of home range use. *Int. Conf. Bear Res. and Manage.* 8, 243-249.
- Sinclair, A.R.E., Fryxell, J.M., Caughley, G., 2006. *Wildlife ecology, conservation, and management*, Blackwell Publishing, Malden, USA.

- Snape, R.T.E., Broderick, A.C., Cicek, B.A., Fuller, W.J., Glen, F., Stokes, K., Godley, B.J., 2016. Shelf life: neritic habitat use of a turtle population highly threatened by fisheries. *Divers. Distrib.*
- Southwood, A.L., Avens, L., 2010. Physiological, behavioral, and ecological aspects of migration in reptiles. *J. Comp. Physiol. B* 180, 1-23.
- Tonani, M., Pinardi, N., Fratianni, C., Pistoia, J., Dobricic, S., Pensieri, S., De Alfonso, M., Nittis, K., 2009. Mediterranean Forecasting System: forecast and analysis assessment through skill scores. *Ocean Sci.* 5, 649-660.
- Tucker, A.D., MacDonald, B.D., Seminoff, J.A., 2014. Foraging site fidelity and stable isotope values of loggerhead turtles tracked in the Gulf of Mexico and northwest Caribbean. *Mar. Ecol. Prog. Ser.* 502, 267-279.
- Wilcove, D.S., Wikelski, M., 2008. Going, going, gone: Is animal migration disappearing? *PLoS Biol.* 6 (7), e188.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164-168.
- Zbinden, J.A., 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.

FIGURE LEGENDS

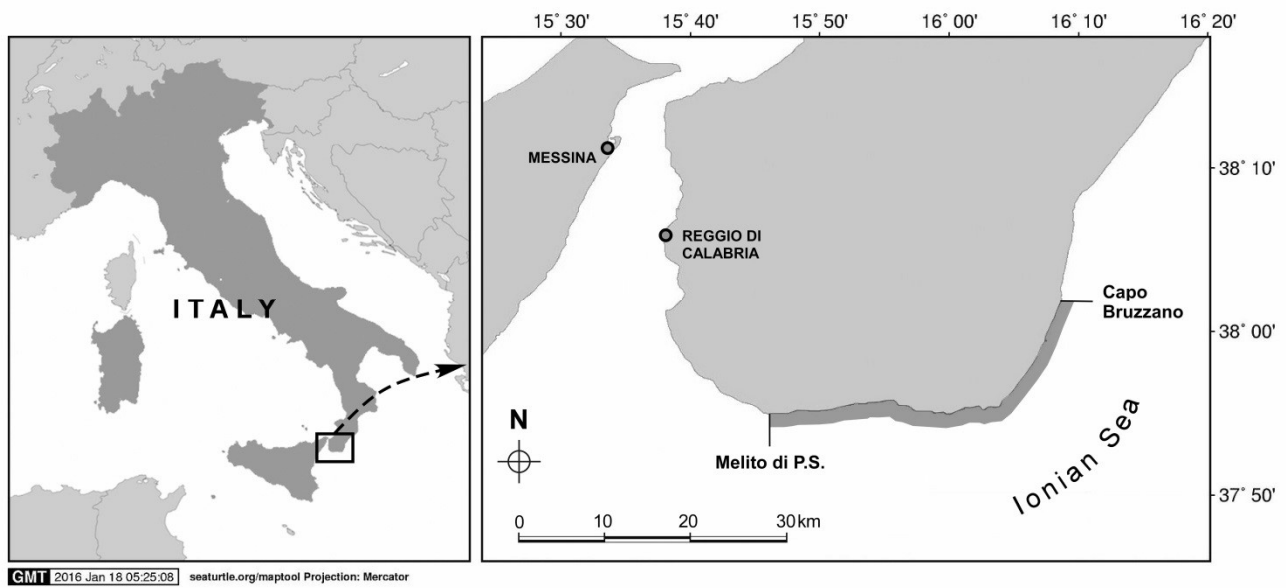


Fig. 1. Location of the study area (dark grey contour), from Capo Bruzzano to Melito di Porto Salvo, at the southernmost tip of the Italian Peninsula. See text for details.

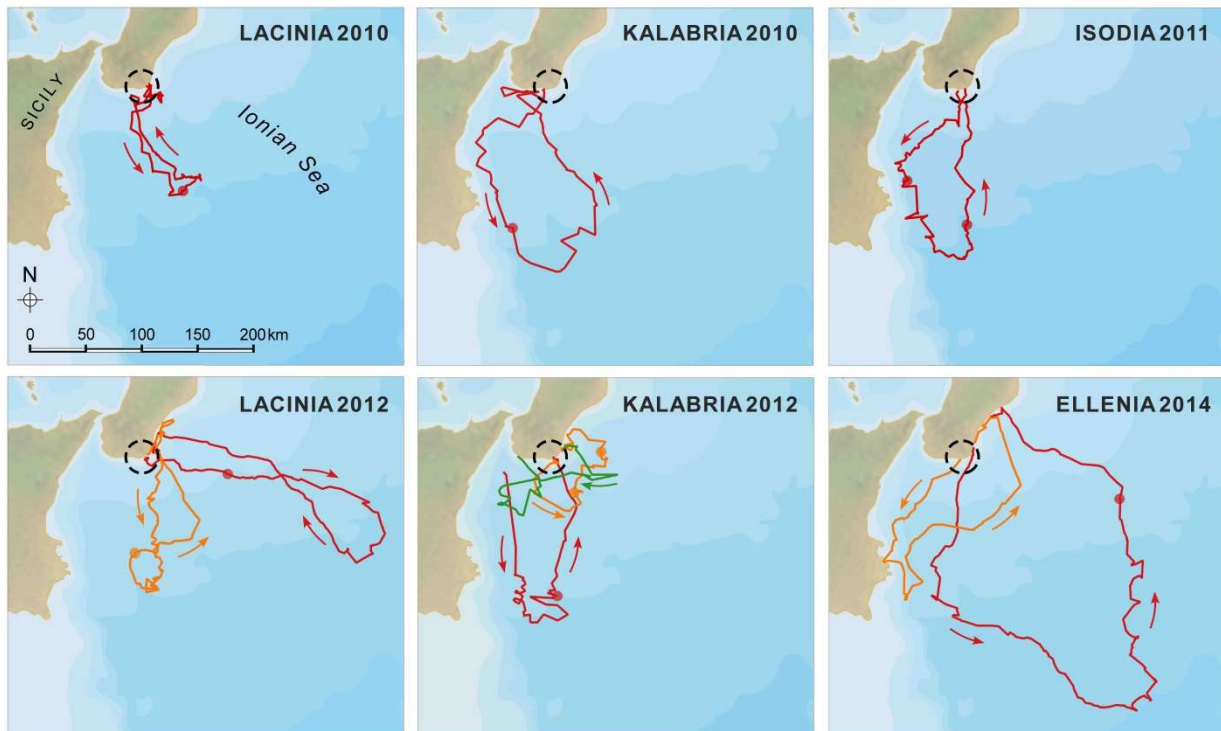


Fig. 2. Inter-nesting movements made by turtles Kalabria (year 2010, 2012), Lacinia (2010, 2012), Isodia (2011), and Ellenia (2014). Dots indicate the CPs determined by the BCPA analysis. Arrows highlight the direction of each loop. The black dashed circle shows the location of the surveyed nesting coast.

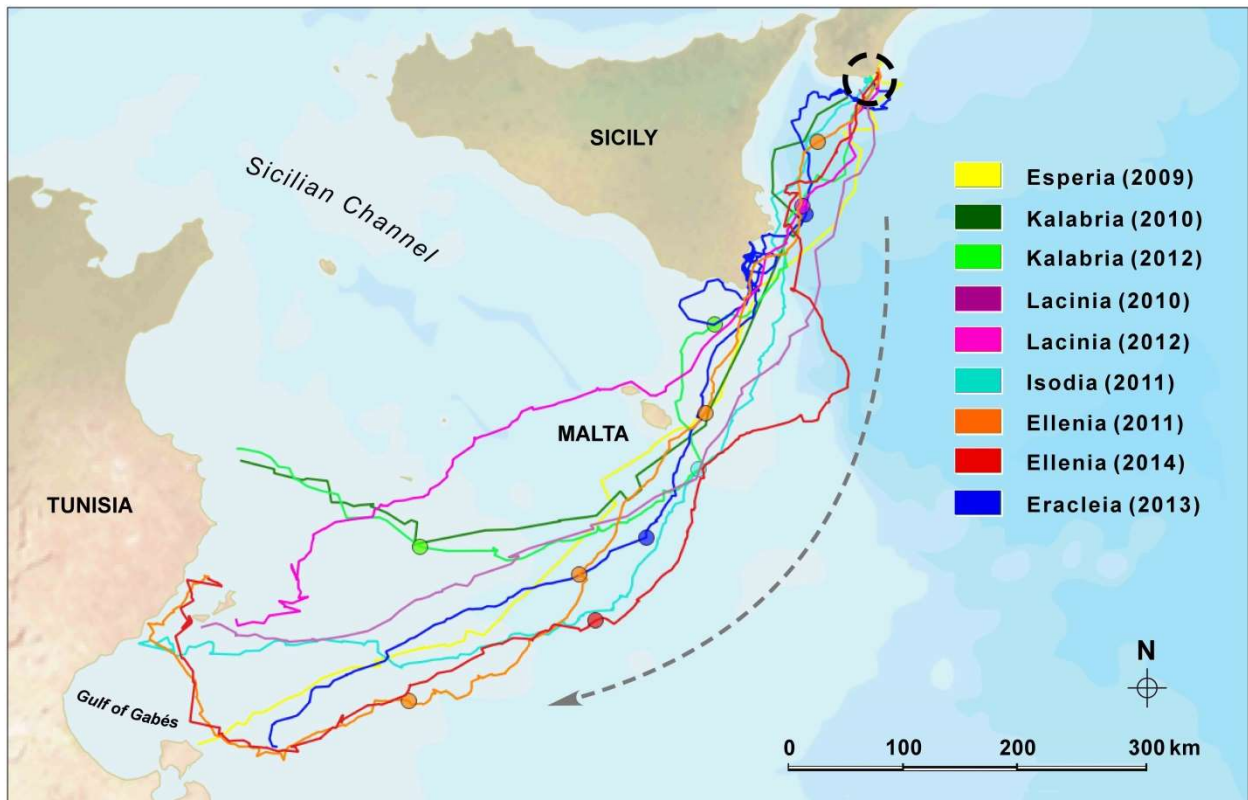


Fig. 3. Post-nesting migrations of turtles *Esperia* (year 2009), *Kalabria* (2010, 2012), *Lacinia* (2010, 2012), *Isodia* (2011), *Ellenia* (2011, 2014), and *Eracleia* (2013), from the Calabrian nesting coast (black dashed circle) towards the Tunisian shelf. Dots indicate the CPs determined by the BCPA analysis. See text for details.

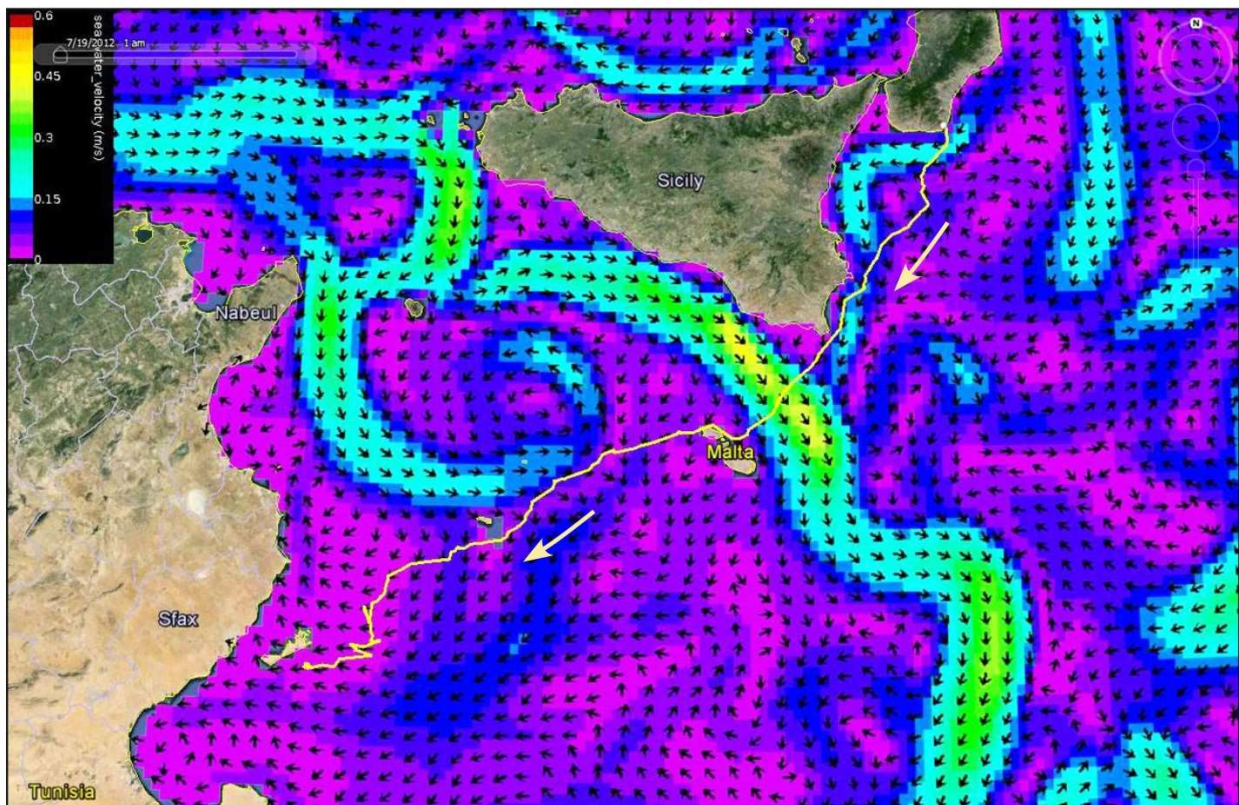


Fig. 4. Ocean current field estimated by the Mediterranean Forecasting System model in the study region for the month of July 2012 (see text for further details). Superimposed is the track of turtle Lacinia that migrated from Calabria in the same month. The south-easterly flow of the Atlantic-Ionian stream (Poulain et al. 2012) is clearly identifiable between southern Sicily and Malta Island. Current velocity is colour coded: small black arrows indicate the current direction.

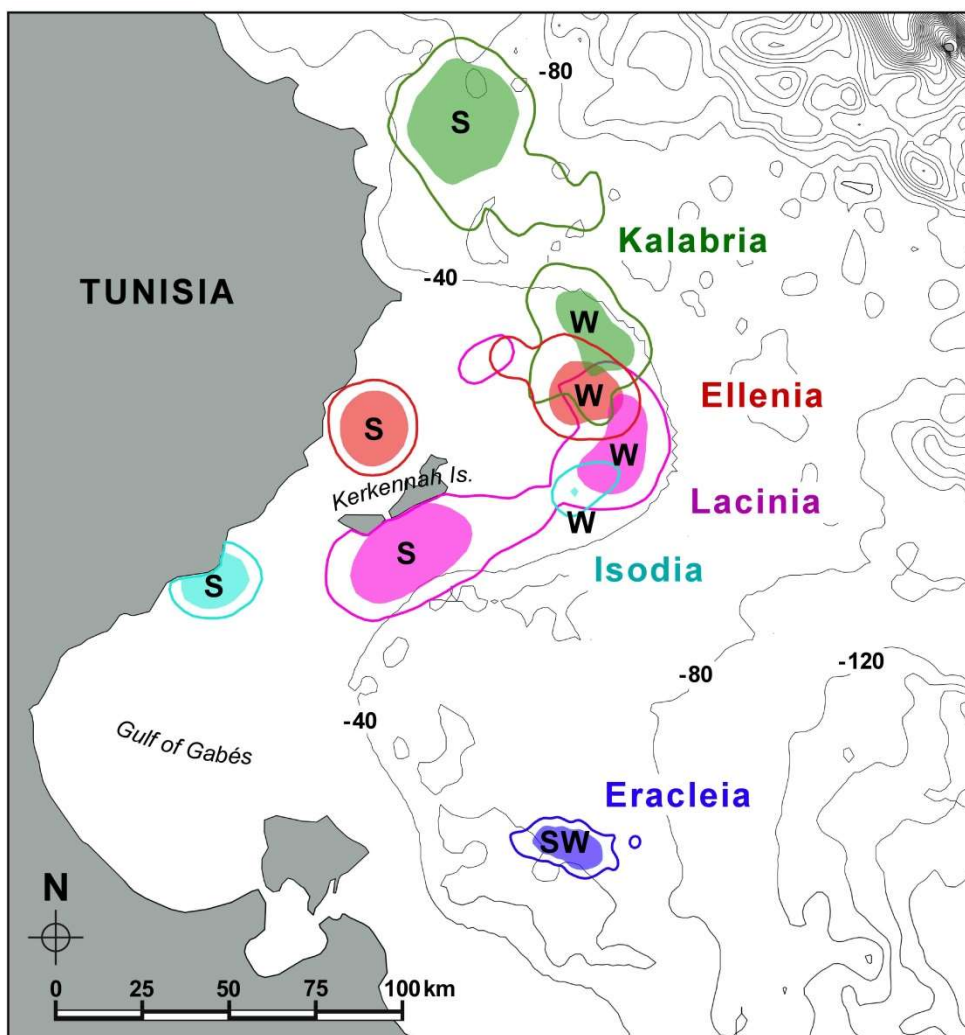
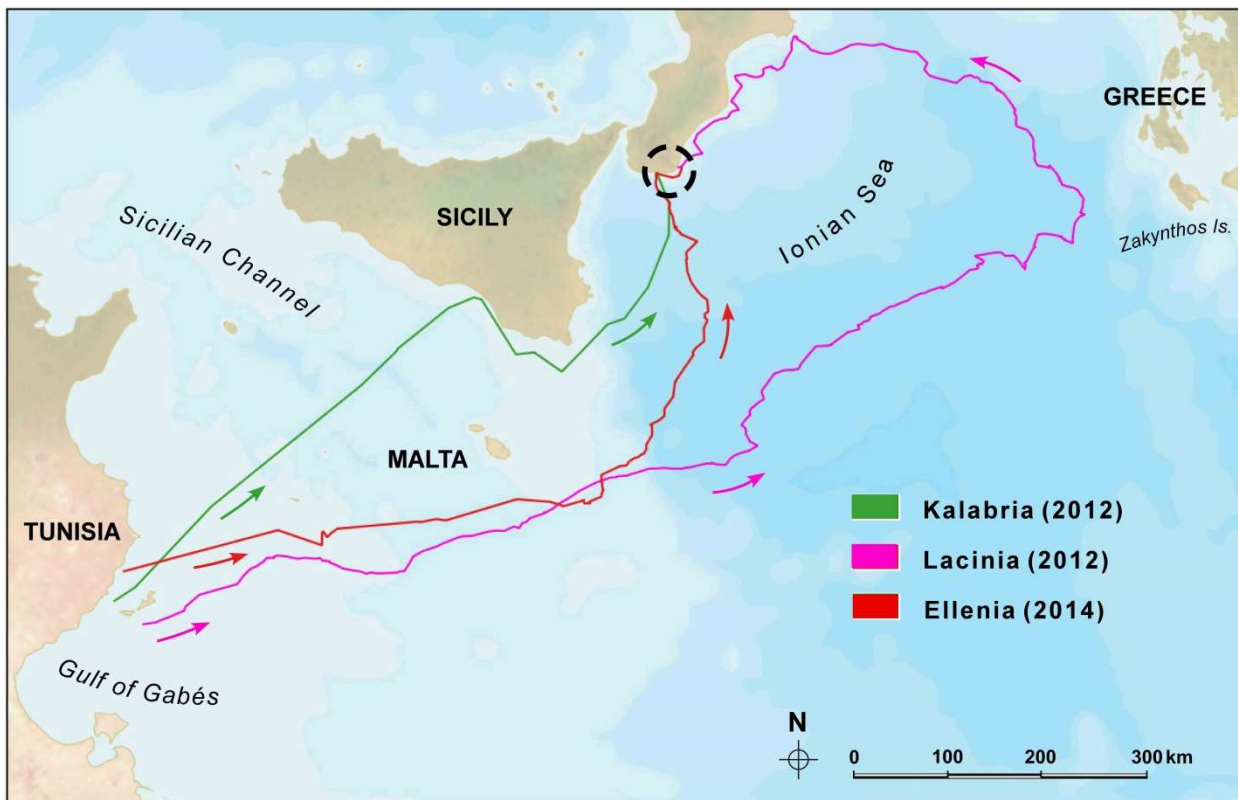


Fig. 5. Summer (S) and winter (W) resident areas of the 5 turtles tracked during their stay at the foraging grounds on the Tunisian shelf. The home ranges (Kernel 95%) are highlighted by continuous contour lines, while the core areas (Kernel 80%) are marked with full colour polygons. Depth contours every 40 metres (ETOPO 1 Bathymetry) are represented.



from the Tunisian foraging areas to the Calabrian nesting coast (black dashed circle). Route direction is shown by arrows.

TABLES

Table 1. Details of tracked turtles, transmitter models and tracking results.

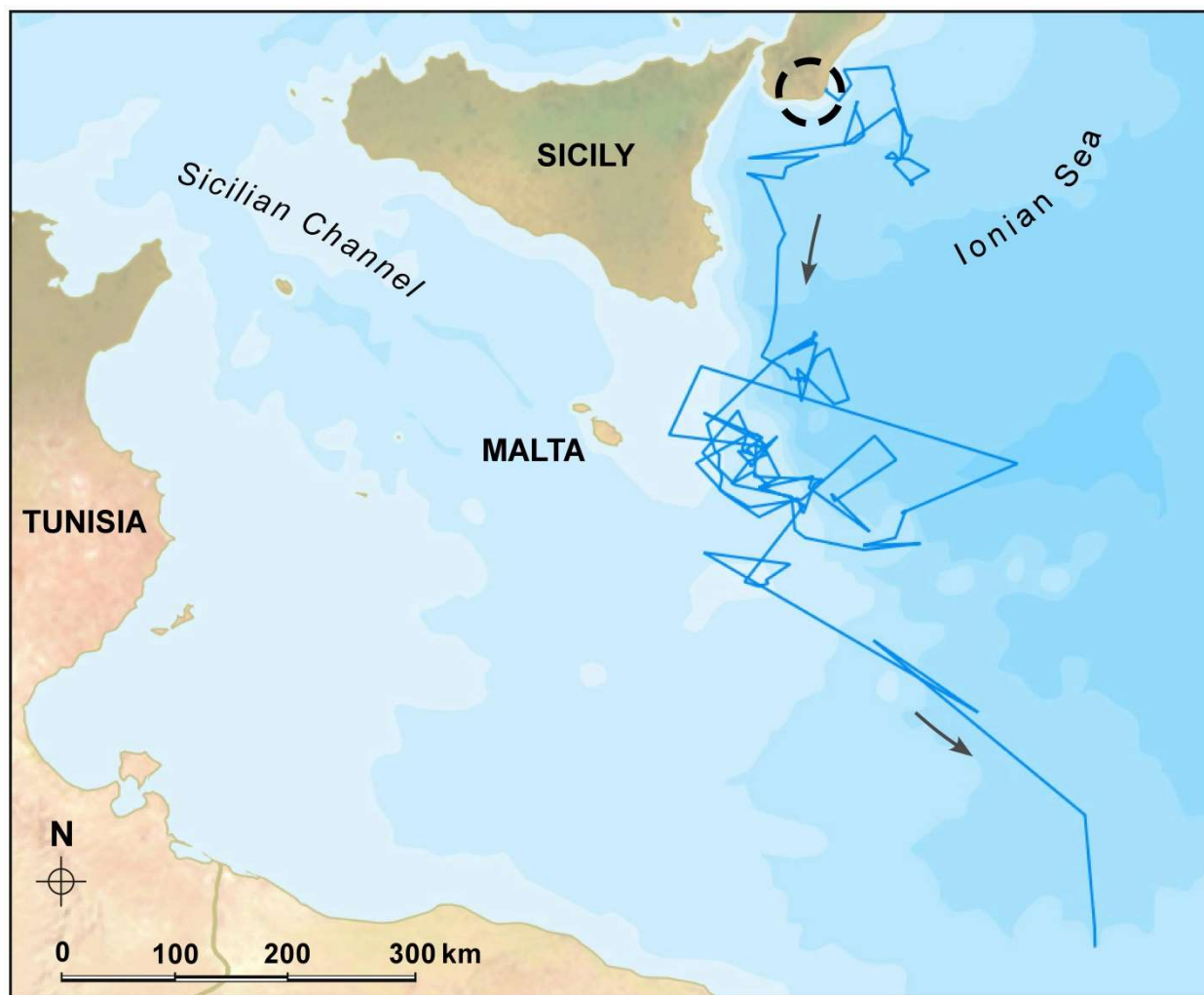
Turtle name	Curved Carapace Length (cm)	Deployment date	Tagging location (Lat, Long)	PTT model	Last location date	Number of tracking days	Travelled distance (km)	Number of locations filtered (total)
Zeffiria	77	16/07/2009	37.990°N, 16.121°E	Telonics, A-410	25/05/2010	313	3605	169 (251)
Esperia	71	29/07/2009	38.019°N, 16.137°E	Telonics, ST20	18/08/2009	20	922	88 (156)
Lacinia	81	04/07/2010	37.942°N, 16.082°E	Sirtrack, Kiwisat 101	30/07/2013	1122	19129	3739 (5241)
Kalabria	76	15/07/2010	37.920°N, 15.955°E	Sirtrack, Kiwisat 101	22/12/2012	891	14192	2575 (3488)
Ellenia	73	08/07/2011	37.942°N, 16.082°E	Sirtrack, Kiwisat 101	08/09/2015	1523	14750	8803 (10400)
Isodia	80	10/07/2011	37.923°N, 16.048°E	Sirtrack, Kiwisat 101	05/07/2012	361	6698	3063 (3946)
Eracleia	73	24/07/2013	37.924°N, 16.062°E	Sirtrack, Kiwisat 202	05/10/2014	439	8540	3286 (4687)

Table 2. Details of the inter-nesting movements tracked in four turtles.

Turtle name	Year	Start	End	Interval (days)	Distance between nesting locations (beeline, km)	Habitat type	Maximum distance from nesting location (km)
Lacinia	2010	4 July	18 July	14	4.3	Oceanic	96
	2012	20 June	6 July	16	7.5	Oceanic/Coastal	215
	2012	6 July	19 July	13	4.4	Oceanic	124
Kalabria	2010	15 July	31 July	16	0.7	Oceanic	159
	2012	18 June	2 July	14	11.9	Oceanic	143
	2012	2 July	15 July	13	11.3	Oceanic	53
	2012	15 July	29 July	14	11.4	Oceanic	56
Isodia	2011	10 July	24 July	14	1.5	Oceanic	147
Ellenia	2014	17 June	7 July	20	26.5	Oceanic	270
	2014	7 July	27 July	20	21.1	Oceanic/Coastal	150

ELECTRONIC SUPPLEMENTARY MATERIAL

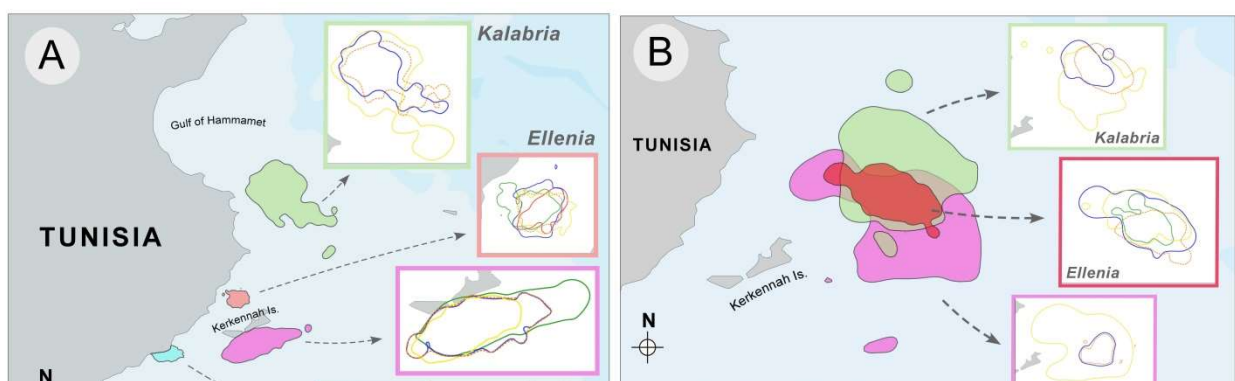
FIGURES



ESM Fig. 1. Post-nesting movements made by turtle Zeffiria. The black dashed circle shows the location of the surveyed nesting coast.



ESM Fig. 2. Tracks of turtles *Esperia* (yellow) and *Kalabria* (green) with the current vectors (blue) estimated along each route. It is evident how currents were generally weak along the route, with a substantial flow being present only southeast of Sicily, in correspondence to the Atlantic-Ionian stream (Fig. 4). The black dashed circle indicates the nesting beaches.



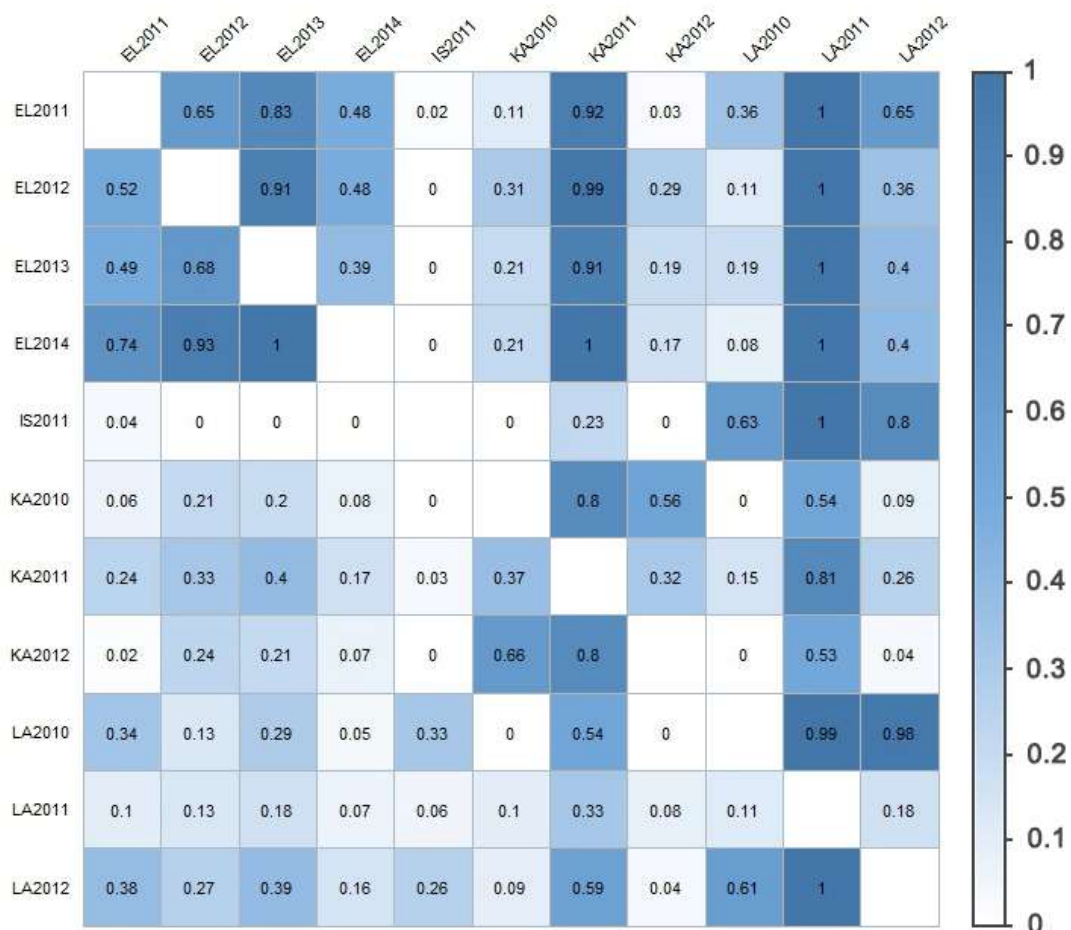
ESM Fig. 3. Seasonal home ranges (Kernel 95%) for the 4 turtles tracked during successive summers (A) and winters (B). Red: turtle Ellenia; cyan: turtle Isodia; green: turtle Kalabria; pink: turtle Lacinia. Inserts show the home ranges of individual turtles in successive years: broken line, first year; yellow line, second year; blue line, third year; green line, fourth year; red line, fifth year. Shading represents bathymetry according to ETOPO 1 Bathymetry.

TABLES

ESM Tab. 1. Sizes of global and seasonal home ranges (HR) and core areas (CA) for the five turtles tracked during their stay at the foraging grounds along the Tunisian continental shelf. The particularly large winter values indicated by asterisks were due to a single looping movement done by the turtle, that abnormally increased HR and CA sizes.

TURTLE NAME	Considered period		Season	HR size (km ²)	CA size (km ²)	Global HR size for season (km ²)	CA size for season (km ²)
	from	to					
LACINIA	01/08/2010	04/11/2011	Summer	781,7	298,1	2207,9	998
	08/11/2010	01/04/2011	Winter	564,9	248,3		
	14/04/2011	04/12/2011	Summer	589,5	278,8	3200,7	1073,4
	10/12/2011	23/04/2012	Winter	4936,9*	2698,2*		
	28/04/2012	19/05/2012	Summer	758,8	284,3	2296,9	1078
	10/12/2012	08/04/2013	Winter	699,4	316,1		
	19/04/2013	30/07/2013	Summer	908,6	438,4	-	-
KALABRIA	14/08/2010	25/12/2010	Summer	1214,1	384,6	2404,4	925,2
	01/01/2011	11/04/2011	Winter	924,4	423,3		
	26/05/2011	06/11/2011	Summer	2244,1	831,1	4309,4	1946,7
	10/11/2011	26/04/2012	Winter	2027,2	883,7		
	14/08/2012	30/11/2012	Summer	1236,9	494,6	1947,1	734,8
04/12/2012	22/12/2012	Winter	800,6	429,4			
ELLENIA	26/07/2011	?	Summer	106,4	46,5	1277,2	638,6
	12/10/2011	10/04/2012	Winter	468,9	206,8		
	13/04/2012	23/08/2012	Summer	136,4	56,6	1192,2	549,9
	17/11/2012	13/04/2013	Winter	647,4	321,9		
	18/04/2013	03/11/2013	Summer	164,2	62,7	1528,6	738,8
	05/11/2013	18/04/2014	Winter	846,5	461,8		
	21/04/2014	24/10/2014	Summer	134,9	57,5	930,4	454,3
	27/10/2014	19/04/2015	Winter	322,7	141,9		
26/04/2015	08/09/2015	Summer	99,9	52,8	-	-	
ISODIA	22/07/2011	31/12/2011	Summer	218,8	98,3	1653,9	781,8
	06/01/2012	23/04/2012	Winter	241,4	118,9		
	26/04/2012	05/07/2012	Summer	134,8	69,2	-	-
ERACLEIA	23/08/2013	11/02/2014	Global	-	-	343	160

ESM Tab. 2. Degree of home range overlapping for four turtles tracked during their stay at the winter foraging grounds. The table shows the proportion (% values) of animal A home range (rows) that is overlapped by animal B home range (columns). For instance the second cell of the first row indicate that the HR of Ellenia in 2012 overlaps for 65% with that of Ellenia in 2011; the second cell of the first column indicate the HR of Ellenia in 2011 overlaps for 52% with that of Ellenia in 2012. Proportion values are colour coded. In rows and columns, the turtle names are indicated by the first two letters (EL: Ellenia; IS: Isodia; KA: Kalabria; LA: Lacinia) for each given year.



ESM Tab. 3. Home range overlapping for four turtles tracked during their stay at the summer foraging grounds. See ESM Tab. 2 for further details.

