

Long-term residence of juvenile loggerhead turtles to foraging grounds: a potential conservation hotspot in the Mediterranean

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ABSTRACT

1. Identifying highly frequented areas is a priority for sea turtle conservation. Although juveniles represent the bulk of the population, a minority of studies have investigated their movement patterns.

2. Six large juvenile loggerhead turtles that were found and released in an important foraging ground in the Mediterranean, the Tunisian continental shelf were tracked. Tracking data were obtained via satellite for periods ranging from 120 to 225 days and allowed the identification of high use areas.

3. All turtles generally performed apparently non-directed, wandering movements in waters with a wide range of seafloor depths. They showed clear residential behaviour to the region with no evident seasonal pattern. Core areas of residence were in the neritic zone or on the edge of the continental shelf, largely overlapping among individuals, and were much smaller than residential oceanic areas reported elsewhere.

4. When integrated into current knowledge, these results suggest an ecological-behavioural model of a gradual shift from a pelagic-vagile to a benthic-sedentary life style with progressive reduction of home ranges.

5. They also highlight an area of the continental shelf and offshore waters as potential core foraging ground for large juvenile loggerhead turtles in the Mediterranean informing future spatial management for loggerhead turtles. Copyright © 2012 John Wiley & Sons, Ltd.

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INTRODUCTION

Conservation of large marine vertebrates is challenging. They are typically slow growing and late maturing and mortality as a result of human actions can severely and rapidly deplete populations (Whitehead *et al.*, 1997). In addition, both as individuals and as populations, they are usually

wide-ranging, potentially facing a great number of threats occurring across their distributional range that may include multiple nations, making the implementation of conservation measures particularly challenging. Detailed knowledge of the distribution, range and habitats of these species is key to generating effective conservation approaches (Gerber and Heppel, 2004; Hamann

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et al., 2010). Distribution of marine vertebrates is, however, generally difficult to study by traditional observational means. In recent years telemetry has made a tremendous contribution towards improving our knowledge on the movements of these species (Cooke, 2008), allowing contextualization of species distribution with anthropogenic threats (Weimerskirch *et al.*, 2006; Cunningham *et al.*, 2009; Baird *et al.*, 2010; Barnett *et al.*, 2011; Witt *et al.*, 2011).

Satellite tracking has rapidly provided information on many aspects of sea turtle ecology (for an overview, see Godley *et al.*, 2008). The integration of this and other approaches is revealing the complex life history of sea turtles (Seminoff *et al.*, 2008; Parker *et al.*, 2009; Maxwell *et al.*, 2011; Witt *et al.*, 2011).

Loggerhead turtles *Caretta caretta* are a particular case in point. They can frequent very distant areas during different life stages (Nichols *et al.*, 2000; Bolten, 2003), feeding on epipelagic or benthic prey in oceanic or neritic zones, respectively (Bjorndal, 1997; Bolten, 2003). In oceanic zones their distribution is mainly affected by oceanographic features (Bolten, 2003; Kobayashi *et al.*, 2008). As a species, loggerhead turtles use trophic resources opportunistically and show great ecological and behavioural plasticity according to the oceanographic and ecological features of the areas they frequent, but as a general tendency juveniles have been shown to frequent more neritic habitats as they grow (Musick and Limpus, 1997; Bolten, 2003; Schroeder *et al.*, 2003; Casale *et al.*, 2008a) with exceptions (Hatase *et al.*, 2002, Hawks *et al.*, 2006; Rees *et al.*, 2010). There are indications from tagging studies on multiple populations that neritic juveniles remain in or at least revisit specific areas (Musick and Limpus, 1997; Casale *et al.*, 2007b). Adults also show extended fidelity to their neritic feeding grounds (Schroeder *et al.*, 2003; Hawkes *et al.*, 2006, 2011; Broderick *et al.*, 2007), which may be the same ones that they recruited to as juveniles (Limpus and Limpus, 2001).

The Mediterranean Sea is severely impacted by many anthropogenic factors such as increasing exploitation of resources, use and degradation of habitats, and pollution (UNEP/MAP/BLUE PLAN, 2009). The main identified threats at sea to sea turtles in the basin are incidental catch in fishing gear, collision with boats, and intentional killing (Tomás *et al.*, 2008; Casale *et al.*, 2010; Casale, 2011) that appear to increase overall mortality

(Casale *et al.*, 2007c, 2010) and as a whole represent a high level of threat (Wallace *et al.*, 2011). Although the Mediterranean basin is rather small in comparison with other oceans, it hosts oceanic and neritic habitats for loggerhead populations belonging to three Regional Management Units (Wallace *et al.*, 2010): the Mediterranean (Casale and Margaritoulis, 2010) and the Atlantic populations, the latter occurring at least in some areas (Carreras *et al.*, 2006; Casale *et al.*, 2008b; Monzon-Arguello *et al.*, 2010).

The identification of high-use areas (hotspots) would represent an opportunity for spatial management, where specific threats might be reduced.

Adult females are the easiest class to tag when they come ashore to nest and a number of studies have documented the routes followed by loggerhead females upon completing their egg-laying cycle in the Mediterranean (Godley *et al.*, 2003; Broderick *et al.*, 2007; Zbinden *et al.*, 2008, 2011), supporting previous findings from tag returns (Margaritoulis *et al.*, 2003). A similar general movement pattern has been shown in adult males (Hays *et al.*, 2010; Schofield *et al.*, 2010). However, these adult movements are intrinsically affected by reproductive behaviour and cannot be necessarily assumed to provide information about movement patterns of juveniles. Juveniles represent the bulk of the population and in particular large juveniles have a high reproductive value (Wallace *et al.*, 2008) and therefore are a priority conservation target. Patterns of distribution and movement of juveniles have been investigated through capture-mark-recapture data, revealing important areas of long-term occurrence (Casale *et al.*, 2007b; Revelles *et al.*, 2008) but such data are intrinsically unable to provide movement patterns between release and re-encounter events. Movements of juveniles have also been investigated through satellite tracking, especially in the oceanic zone of the western Mediterranean. Quite a large variety of movements have been shown, that often ranged over wide areas, and have sometimes been shown to be affected by currents, and in some cases it appears that individuals are making an active choice to remain within a certain area (Bentivegna, 2002; Cardona *et al.*, 2005, 2009; Revelles *et al.*, 2007a, 2007b; Eckert *et al.*, 2008).

To complement previous work, this study investigated movement patterns of large juveniles in the central Mediterranean area between Italy, Tunisia and Libya, a peculiar area where different potential turtle foraging habitats are close to each

other and the same turtle can frequent both neritic and oceanic habitats (Casale *et al.*, 2008a). Besides providing insights into the general turtle behaviour, information about turtle distribution in this area is of direct interest due to the high incidence of turtle bycatch by different fishing gears and the high fishing effort occurring in the central Mediterranean (Casale *et al.*, 2007a; Jribi *et al.*, 2007, 2008).

METHODS

Satellite tags were deployed on six loggerhead turtles in the period between 2002 and 2008 (Table 1). All turtles were found in the neritic waters of the continental shelf off Tunisia. Turtle A was found while floating at sea, while the others were captured by bottom trawlers. All turtles were healthy at the time of capture and were landed at Lampedusa Island, Italy (42°40'N, 16°50'E), in the centre of the study area (Figures 1, 2, and 3). Their curved carapace length notch-to-tip (CCL) (Bolten, 1999) was measured. Argos-linked platform terminal transmitters (PTTs; see Table 1 for models) were attached on the second vertebral carapace scute with a two-part epoxy resin (Power Fasteners, Netherlands). Turtles were kept and fed in tanks of sea water for a period ranging from 3 to 14 days. All were released in a healthy condition from the shores of Lampedusa. Duty cycle was always on for all turtles except turtle F where it was 12 h on/36 h off.

PTT locations were determined by the Argos Service (www.argos-system.org) and data were automatically downloaded by the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley, 2005). STAT also provided seafloor depth and sea surface temperature (SST) for each determined location (for details see Coyne and Godley, 2005).

Argos locations are categorized into seven location classes (LCs) and we selected only the four with the highest accuracy (from higher to lower accuracy: LC 3, 2, 1, A) as recommended by specific studies on LC accuracy (Hays *et al.*, 2001; Royer and Lutcavage, 2008; but see Witt *et al.*, 2010).

In order to study general movement patterns and preferred areas, a maximum of one fix per day was selected. For days with more than one fix, the one with the highest accuracy LC was chosen and if more than one had this LC, the one closest to midday was chosen (Zbinden *et al.*, 2008).

Locations were plotted and analysed by ArcGIS 9.2. High use areas were identified by Kernel density estimates (KDE) with 50% and 25%

Table 1. Curved carapace length (CCL), platform terminal transmitters (PTT), dates and number of fixes of six loggerhead turtles tracked in the Mediterranean. Max displacement: from release place, Lampedusa island

Turtle	CCL (cm)	PTT	Deploy date	Last fix date	Number of tracking days	Number of day fixes	Total distance covered (km)	Max displacement (km)	KDE 50% (km ²)	KDE 25% (km ²)
A	75.3	Satellite relay data logger - Sea Mammal Research Unit, UK	24-Nov-2002	7-Jul-2003	225	41	1785	446	60797	22604
B	69.2	Telonics ST-6, Arizona USA	1-Feb-2003	8-Jul-2003	157	112	2805	215	14756	5935
C	57.0	Telonics A-410, Arizona USA	6-Mar-2007	23-Sep-2007	201	151	3478	388	34366	14178
D	54.5	Telonics A-410, Arizona USA	6-Mar-2007	29-Aug-2007	176	118	1966	200	16813	7300
E	54.5	Telonics A-210, Arizona USA	25-Mar-2007	23-Jul-2007	120	75	1515	212	22276	9412
F	62.5	Telonics A-1010, Arizona USA	11-Mar-2008	9-Oct-2008	212	85	1630	450	8702	3188

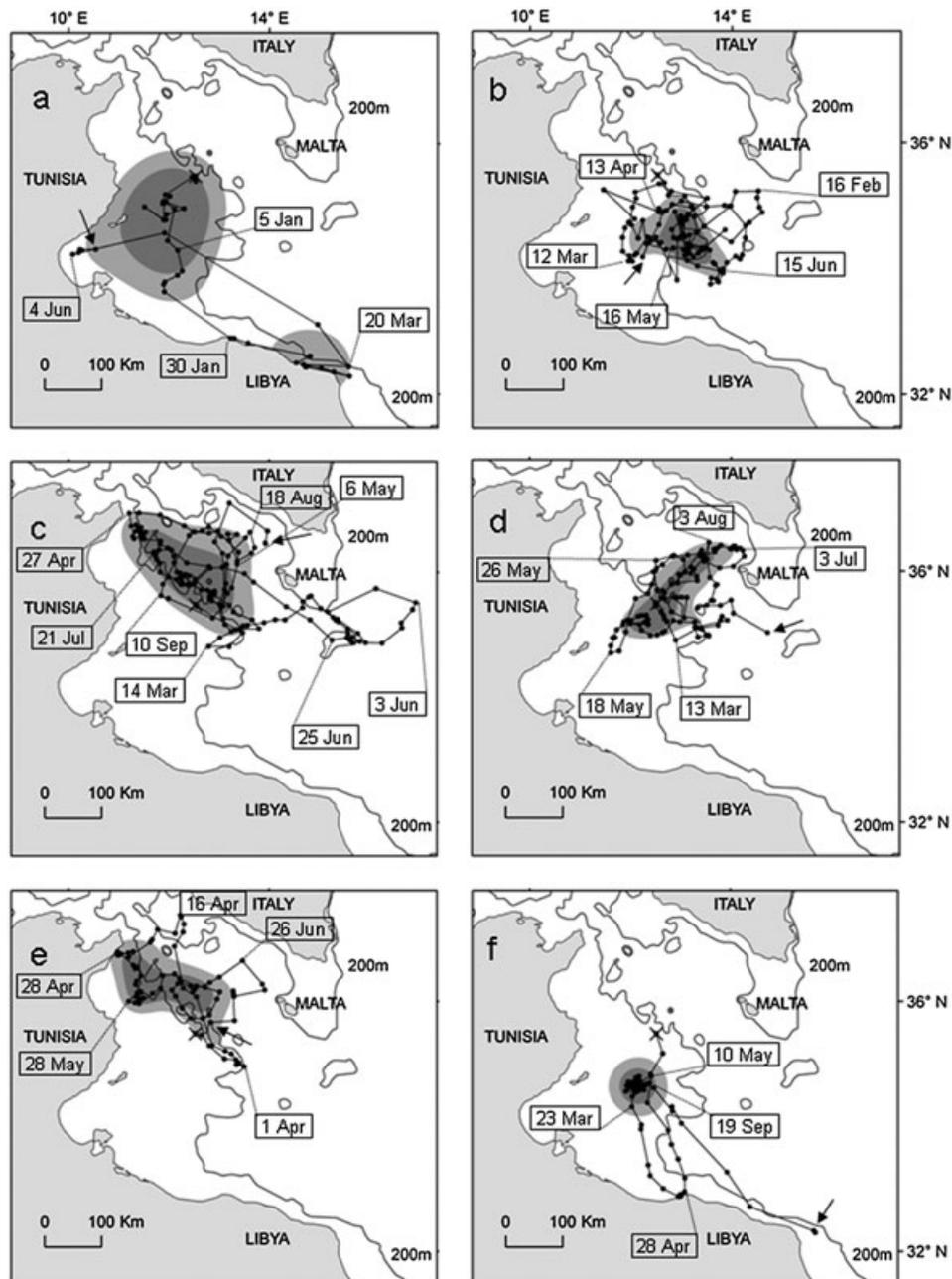


Figure 1. Tracks of six loggerhead turtles (A to F) in the central Mediterranean. Cross: Lampedusa island (release site); arrow: last position (see Table 1 for dates of release and last position). Light and dark grey: KDEs 50% and 25% UD, respectively.

utilization distribution (UD), obtained with the Home Range Tools extension for ArcGIS (HRT) (Rodgers *et al.*, 2007). The smoothing parameter h was calculated with the reference bandwidth method (h_{ref}) in HRT. Minimum distance travelled and minimum speed between fixes was calculated assuming straight-line movements.

RESULTS

The six tracked turtles ranged from 54.5 to 75.3 cm CCL (mean: 62 ± 9 cm) (Table 1). None showed

adult male sexual dimorphism (Casale *et al.*, 2005) and since on average Mediterranean female loggerhead turtles mature at a size larger than 70 cm CCL, although the smallest adult female reported from the Mediterranean is 60 cm CCL (Margaritoulis *et al.*, 2003), it is likely that most of the tracked turtles were still immature. Turtles were tracked for a period ranging from 120 to 225 days (mean: 182 ± 39 days) for a total of 1091 days, of which 582 with post-filtering day-fixes, and their minimum distance travelled ranged from 1515 to 3478 km (mean: 2197 ± 777 km) (Table 1).

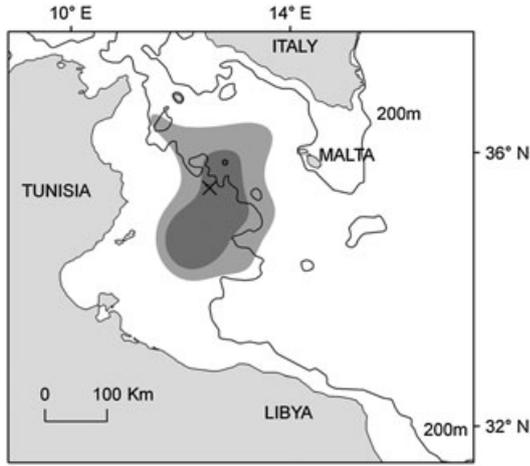


Figure 2. KDE 50% and 25% UD of all fixes combined of six loggerhead turtles in the central Mediterranean. Cross: Lampedusa Island (release site).

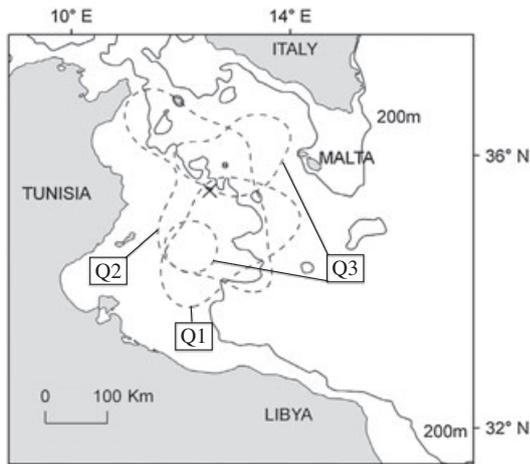


Figure 3. KDEs 50% UD of all fixes combined of six loggerhead turtles in the central Mediterranean, per year quarter, except for Oct–Dec because of its small sample size. Q1: Jan–Mar ($n=100$ fixes); Q2: Apr–Jun ($n=315$ fixes); Q3: Jul–Sep ($n=148$ fixes). Cross: Lampedusa Island (release site).

Average speed for the entire period ranged from 7.7 and 17.9 km day⁻¹, while the mean average speed between consecutive fixes was below 1.0 km h⁻¹ for all turtles, with a maximum of 3.63 km h⁻¹ (Table 2). As shown in Figure 1, all turtles generally performed non-directed, wandering movements

over medium-large distances, usually following looping routes. Maximum displacement from the release site ranged from 200 to 450 km (mean: 319 ± 122 km) (Table 1). KDEs for 50% and 25% UD of individual turtles are shown in Figure 1 and those of all turtles combined are shown in Figure 2 (see Table 1 for values). KDEs can be overestimated in cases of few or dispersed locations and values are provided for comparisons rather than for exact home range estimation. No latitudinal or longitudinal difference of KDE for 50% UD of all turtles combined was observed among three year quarters (Jan–Mar; Apr–Jun; Jul–Sep) (Figure 3). SSTs at turtle locations ranged between 13.9 and 28.8 °C (Table 2, Figure 4). Turtles frequented areas over a wide range of seafloor depths (Table 2, Figure 5). If we consider neritic zones as those below 200 m, the conventional limit of the continental shelf, individual turtles were in neritic areas for between 13.3 and 94.0% of their locations (Table 2). Two turtles (A and F) predominantly frequented the neritic zone (>90% of their daily fixes), while turtle C predominantly frequented the oceanic zone (13.3% of daily fixes in the neritic zone). The other three turtles demonstrated somewhat intermediate levels. The three turtles for which the majority of the fixes were in neritic waters were larger (62.5; 69.2; 75.3 cm CCL) than those with a majority of oceanic fixes (54.5; 54.5; 57.0 cm CCL), although direct correlation between these two variables was not statistically significant (Spearman rank test; $R=0.64$; $P=0.17$; $n=6$), possibly a type II statistical error.

The two turtles that mostly frequented the neritic zone (A and F) were also the ones with the longest maximum displacement (Table 1). They frequented two different areas, a long tract of Libyan coast and offshore areas in the wider Tunisian continental shelf, and although they often demonstrated wandering movements, they also showed some short directional movements when moving back and forth between the two areas

Table 2. Speed, depth of sea bottom, and temperatures at locations of six loggerhead turtles tracked in the Mediterranean

Turtle	Speed between fixes (km h ⁻¹) mean ± SD (range; n)	Overall mean speed (km day ⁻¹)	Depth at fixes (m) mean ± SD (range; n)	Fixes at <200m	SST at fixes (°C) mean ± SD (range; n)
A	0.48 ± 0.48 (0.02-2.04; 40)	7.9	73 ± 117 (4-710; 40)	92.5%	17.8 ± 2.6 (14.8-26.9; 40)
B	0.92 ± 0.75 (0.14-3.63; 111)	17.9	198 ± 137 (40-605; 110)	63.6%	18.8 ± 4.2 (13.9-27.3; 110)
C	0.75 ± 0.47 (0.06-3.24; 150)	17.3	497 ± 568 (55-3863; 150)	13.3%	21.9 ± 4.1 (15.2-27.8; 147)
D	0.56 ± 0.40 (0.04-2.17; 117)	11.2	377 ± 306 (5-1409; 118)	36.4%	21.2 ± 4.0 (15.8-28.8; 114)
E	0.64 ± 0.38 (0.01-1.82; 74)	12.6	334 ± 258 (47-1196; 75)	40.0%	19.6 ± 3.3 (14.9-27.5; 75)
F	0.34 ± 0.33 (0.01-1.43; 84)	7.7	72 ± 58 (12-396; 83)	94.0%	22.6 ± 4.3 (15.5-28.3; 79)

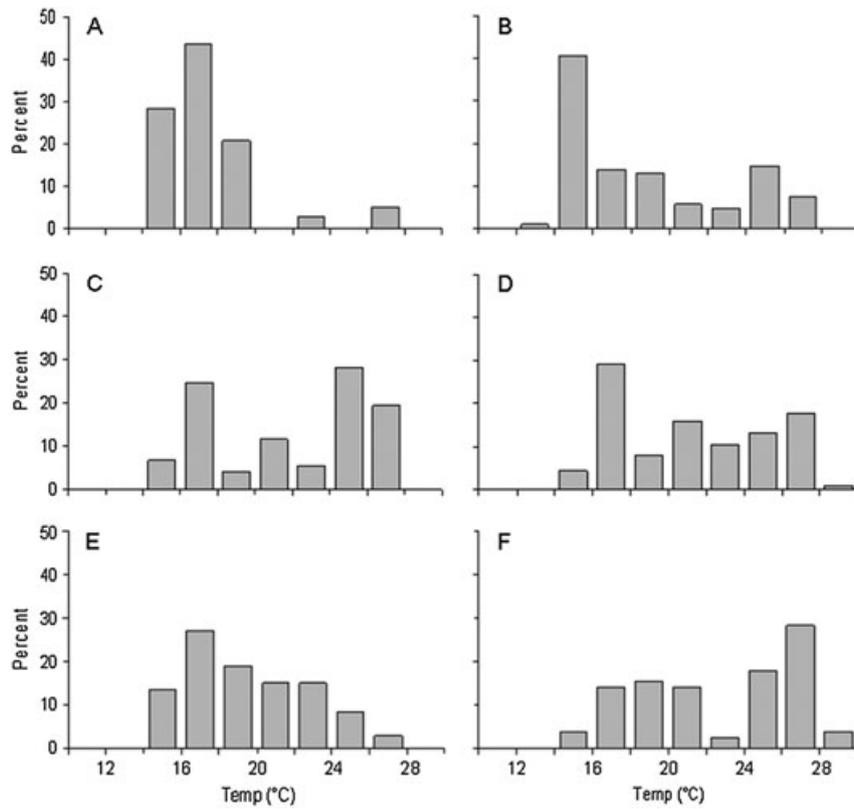


Figure 4. Frequency distribution of SST at location of six loggerhead turtles in the central Mediterranean (A to F) ($n = 559$).

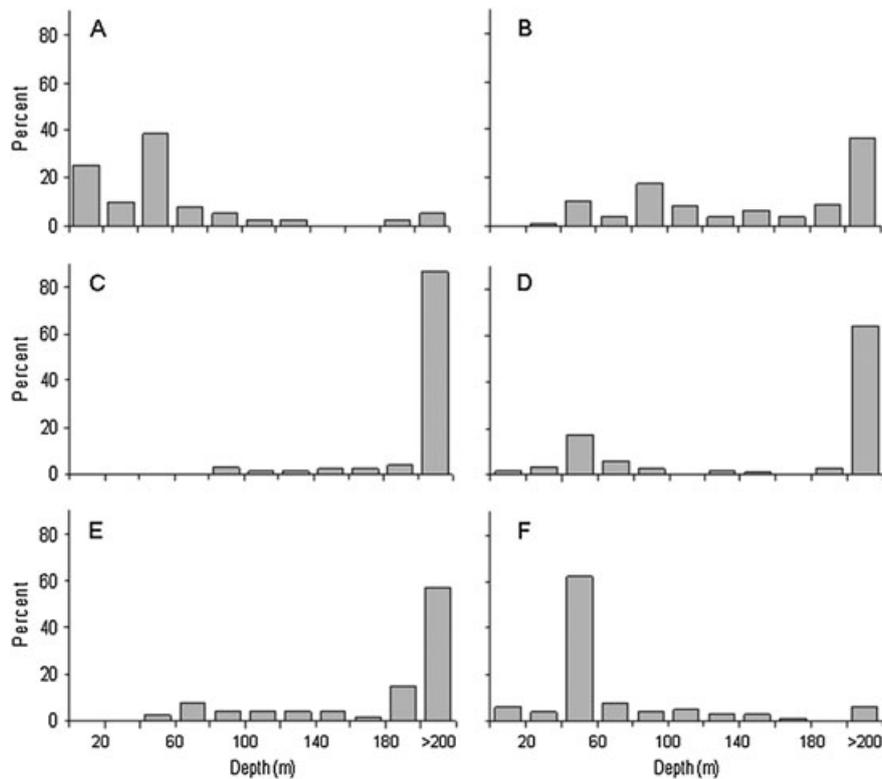


Figure 5. Frequency distribution of depth at location of six loggerhead turtles (A to F) in the central Mediterranean ($n = 570$).

(Figures 1(a) and 1(f)). The other four turtles (B–E) only made wandering movements, often across the 200 m isobath, with alternation of loops and straight segments, with turtle C also having an eastward detour over oceanic waters offshore of Malta (Figure , 1(b) to 1(e)). The latter group of turtles had an overall swimming speed (mean: 14.7 km day⁻¹; SD: 3.34 km day⁻¹) higher than the former group (mean: 7.8 km day⁻¹; SD: 0.17 km day⁻¹) (Table 2).

DISCUSSION

An increasing number of novel insights into sea turtle spatial ecology are becoming available thanks to the unique opportunities given by satellite tracking technology (Godley *et al.*, 2008). The six large juveniles found in neritic waters and tracked in this study provide additional insights to better understand the complex behavioural ecology pattern of the loggerhead turtle.

All six turtles appeared to be resident in the central Mediterranean area, regardless of their preference for neritic or oceanic zones. The distance travelled would have allowed turtles to reach most, if not all areas of the Mediterranean, some with potentially better trophic opportunities or temperature regimes. On the contrary, all turtles remained in the central Mediterranean area during the whole tracking period. Moreover, no general seasonal pattern was observed, and this is consistent with other two studies in the Mediterranean, one of which observed no preference for warmer waters at temperatures as low as 12.5 °C (Hochscheid *et al.*, 2007; Revelles *et al.*, 2007a). However, cases of seasonal movements in the Mediterranean are known, for instance the emigration from a small area in the northernmost part of the north Adriatic (north of 45°N), where temperatures in winter drop below 11–12 °C (Lazar *et al.*, 2003) or the southward movement recorded in satellite tracked adult females leaving the north Adriatic Sea in the cold period (Zbinden *et al.*, 2008, 2011) and in juveniles in the western Mediterranean (Cardona *et al.*, 2009). The tracked turtles frequented areas with temperatures of minimum 13.9 °C. Although some differences in the range and means of temperature experienced were observed among tracked turtles, they are not apparently due to different movement patterns.

Fidelity of adult females to neritic foraging grounds was observed through flipper tagging (Limpus *et al.*, 1992; Limpus and Limpus, 2001)

and through satellite tracking of successive postnesting migrations in the Mediterranean (Broderick *et al.*, 2007) and elsewhere (Marcovaldi *et al.*, 2010). It can also be inferred in the long term from distinctive isotope profiles (Zbinden *et al.*, 2011).

Long-term residence of juveniles to neritic foraging grounds have been observed from tag returns (Casale *et al.*, 2007b; Revelles *et al.*, 2008). However, these observations could not exclude turtles frequenting other areas between release and re-encounter locations, and the present results, together with another satellite tracking study on the neritic Spanish waters (Cardona *et al.*, 2009) provide complementary indications of a constant residence of juveniles in neritic grounds. Indications of juvenile residence in oceanic areas are more ambiguous. A degree of permanence in the same area was observed through satellite tracking in some cases (Revelles *et al.*, 2007a) but not in others (Bentivegna, 2002; Cardona *et al.*, 2005, 2009; Eckert *et al.*, 2008) and it was also indicated by tag returns (Casale *et al.*, 2007b). This permanence can be explained by a mix of surface circulation patterns and active area selection (Revelles *et al.*, 2007b). In general, resident areas of juveniles in oceanic zones are much wider than in neritic zones (Revelles *et al.*, 2007b; Cardona *et al.*, 2009) and the same was observed in adults (Hawkes *et al.*, 2006; Schofield *et al.*, 2010).

However, in the Mediterranean there is a large variability with evidence of large juveniles showing no residence, neither in oceanic nor in neritic grounds, such as juveniles wandering across wide oceanic areas (Eckert *et al.*, 2008; Cardona *et al.*, 2009) and large juveniles tagged and then re-encountered in distant areas (Casale *et al.*, 2007b). A possible explanation is that some individuals follow an alternative 'nomadic' pattern (Casale *et al.*, 2007b), i.e. continuously moving among distant areas with no evident settlement and residence. The factors inducing such different behaviours are unknown and could be environmental, population or individual based. For instance, within the same population, different individuals may display a different movement pattern (Watanabe *et al.*, 2011).

Two turtles (A and F) frequented almost exclusively the continental shelf area, while three (C, D, E) mostly frequented the oceanic zone. This suggests that the former fed mainly on benthic prey while the latter mainly on pelagic prey although, naturally, even when on the continental shelf, turtles might not dive to the sea floor and

they might feed on pelagic prey only as they do when they are in oceanic zones. However, turtles C, D and E were caught by bottom trawlers and this indicates that they were on the sea floor when captured, suggesting a mixed strategy of both benthic and epipelagic feeding. Indeed, dietary analyses (Casale *et al.*, 2008a) showed that turtles in this area are opportunistic feeders and feed on benthic prey if they have the opportunity to do so, beginning at a very small size (e.g. 26 cm CCL). Although six turtles represent a small sample, the observed tendency of frequenting neritic areas at larger size fits the model of a gradual increase in the use of benthic trophic resources as the turtle grows (Casale *et al.*, 2008a).

The residence areas determined in this study were in the neritic zone or between neritic and oceanic zones and they were much smaller than residential oceanic areas reported elsewhere (Revelles *et al.*, 2007a, 2007b). Even smaller home ranges at neritic foraging grounds, and also smaller than turtles A and F which were the most neritic of the present study, have been observed in post-nesting females in Brazil and Greece (Marcovaldi *et al.*, 2010; Schofield *et al.*, 2010). This suggests that when turtles start feeding upon benthic prey in neritic/edge areas, they tend to reduce their home ranges and continue to do so as they grow. In turn, this would indicate that turtles follow a minimal-area strategy of optimal foraging (Mitchell and Powell, 2004) with the reduction in home ranges being possibly due to the higher availability and energy content of the benthic prey accessible in the neritic zone than of the epipelagic prey that are the only available ones for loggerheads in the oceanic environment.

Together with a previous ecological model (Casale *et al.*, 2008a), the present results and those from another study in the western Mediterranean (Cardona *et al.*, 2009) suggest an ecological-behavioural model of a gradual shift from a pelagic-vagile to a benthic-sedentary life style with progressive reduction of home ranges, that can explain most of the current information on the movements of loggerheads in the Mediterranean. In particular, the oceanographic features of the Mediterranean, with a great extension of oceanic-neritic edges, would produce an 'edge effect' that may favour opportunistic feeding, early frequentation of neritic feeding grounds, together with early settlement and residence. In areas where neritic and oceanic zones are more clearly separated and/or distant (e.g. at the borders of oceans), the oceanic/neritic shift of

juvenile loggerheads may be more clear-cut (Bolten, 2003). Comparable investigations at other 'edge' zones of the Mediterranean Sea (e.g. the Adriatic, Aegean, Levantine Seas) are needed in order to assess whether it is a reliable general model or a peculiarity of the central and western Mediterranean. In any case, such an ontogenetic shift would not be an irreversible transition, as a return to an oceanic life style has been shown to occur in both large juveniles (McClellan and Read, 2007) and adults can be oceanic or switch between oceanic and neritic habitats (Hatase *et al.*, 2002; Hawkes *et al.*, 2006; Rees *et al.*, 2010).

In addition to coastal areas at nesting sites (Schofield *et al.*, 2009), identifying highly frequented areas off shore is a key priority for turtle conservation. For instance, if fishing effort or boat traffic, two of the major threats to sea turtles in the Mediterranean (Casale *et al.*, 2010; Casale, 2011), could be adequately managed in a highly frequented area or displaced to less frequented areas, the overall anthropogenic turtle mortality would decrease.

The study area is an important foraging ground for the most important turtle rookeries of the Mediterranean including western Greece, Crete and Cyprus (Margaritoulis *et al.*, 2003; Broderick *et al.*, 2007; Casale *et al.*, 2008b; Zbinden *et al.*, 2008). Therefore, the high level of incidental captures in the area (Casale *et al.*, 2007a; Jribi *et al.*, 2007, 2008) represents a major threat to the Mediterranean loggerhead turtle population. The present tracking results highlight the importance of the area around the Pelagie Islands (Lampedusa and Linosa, Italy) on the edge of the continental shelf and the southern area on the continental shelf as a core foraging ground for loggerhead turtles in the central Mediterranean. This represents a preliminary indication of the possible efficacy of a spatial management scheme for turtle conservation in the area, but needs to be confirmed and better defined by further research with a higher number of individuals.

Turtles A and F moved along the coastline while heading to distant areas. Together with similar data on adult females (Broderick *et al.*, 2007), the present tracks of juveniles suggest that the north African coast is an important pathway for loggerhead turtles in the Mediterranean, at least for turtles frequenting neritic waters, and as such represents a further critical area where specific attention and protection is needed (Broderick *et al.*, 2007).

In conclusion, these results add to a growing body of evidence suggesting the existence of a

hotspot for loggerhead sea turtles in the central Mediterranean, with particular reference to neritic or edge zones. The importance for sea turtle conservation of such hypothetical hotspots deserves additional and specific research effort on the fine scale movements of juvenile turtles, which represent the bulk of the population. In particular, priorities for future research are: (i) to increase the number of large loggerhead juveniles tracked by satellite telemetry in the study area, in order to confirm and define hotspots in one of the most important foraging areas for this species in the Mediterranean; (ii) to acquire information on adult home ranges while foraging in this area, in order to identify a possible common pattern; (iii) to perform satellite tracking with large loggerhead turtle juveniles found in neritic waters of other Mediterranean areas, on large shelves and shelf edges, in order to test the behavioural ecology model suggested and to identify additional possible conservation hotspots.

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