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ORIGINAL PAPER

Foraging grounds, movement patterns and habitat connectivity of juvenile loggerhead turtles (*Caretta caretta*) tracked from the Adriatic Sea

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Abstract Knowledge about migratory routes and highly frequented areas is a priority for sea turtle conservation, but the movement patterns of juveniles frequenting the Adriatic have not been investigated yet, although juveniles represent the bulk of populations. We tracked by satellite six juvenile and one adult female loggerhead from the north Adriatic. The results indicated that loggerhead juveniles (1) can either show a residential behaviour remaining in the Adriatic throughout the year or perform seasonal migrations to other areas, (2) can remain even in the coldest, northernmost area during winter, (3) can frequent relatively small foraging areas, (4) mostly frequent the eastern part of the Adriatic, and (5) follow preferred migratory routes along the western and eastern Adriatic coasts. The movements of the adult turtle also revealed (6) a behavioural polymorphism in Mediterranean adults, which included a lack of area fidelity and connection between distant neritic foraging grounds.

Introduction

During their lives, loggerhead sea turtles (*Caretta caretta*) can frequent disparate areas, feeding on epipelagic or benthic prey in oceanic and neritic zones (Bjorndal 1997; Nichols et al. 2000; Bolten 2003). This endangered species (IUCN 2011) exhibits a highly plastic life history, with a general tendency of juveniles to frequent more neritic habitats as they grow (Musick and Limpus 1997; Bolten 2003; Casale et al. 2008a). Adult loggerheads have been found to show fidelity to their neritic feeding grounds (Broderick et al. 2007; Schofield et al. 2010; Zbinden et al. 2011), which may be the same ones they recruited to as juveniles

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(Limpus and Limpus 2001; Casale et al. 2007a). Given the scale of movements and the different habitats utilised during their lives, information about migratory routes, habitat use and most frequented areas is key for planning their conservation (Hamann et al. 2010).

Loggerheads represent the most abundant turtle species in the Mediterranean Sea, with reproductive habitats concentrated in the eastern basin and dispersing widely in the other areas, including the western part, both as juveniles and as adults (Casale and Margaritoulis 2010). Within the Mediterranean, the Adriatic Sea has been identified as an important marine area for sea turtles and notably for loggerheads since the other two turtle species frequenting the Mediterranean, the leatherback (*Dermochelys coriacea*) and the green turtle (*Chelonia mydas*), occur in relatively low numbers in the Adriatic (Casale et al. 2003; Lazar et al. 2004a, 2008). Loggerhead nesting activity is absent or extremely low along the Adriatic coasts, with just a few nests recorded (Mingozzi et al. 2007), but the Adriatic is clearly an important foraging ground for loggerhead turtles of all life stages, as shown by a number of different findings. First, high numbers of turtles are incidentally caught by fishing gear (Lazar and Tvrtković 1995; Affronte and Scaravelli 2001; Casale et al. 2004), with over 11,000 captures per year mostly by bottom trawlers (Casale 2011). Second, tag recoveries and satellite tracking of adults tagged whilst breeding in Zakynthos (Greece) showed that the Adriatic is one of the few foraging grounds for adult loggerheads from this rookery (Margaritoulis et al. 2003; Lazar et al. 2004b; Zbinden et al. 2008, 2011; Hays et al. 2010b; Schofield et al. 2010). Third, medium- to long-term permanence of juvenile loggerhead turtles in the area has been shown by flipper tag returns (Casale et al. 2007a). Finally, the Adriatic, and its southern part in particular, hosts an important developmental area for juveniles in the first years of life, probably hatched in Greece (Casale et al. 2010), as suggested by dispersal models based on sea currents (Hays et al. 2010a). Whilst the Mediterranean is frequented by loggerhead turtles belonging to two regional management units (Wallace et al. 2010)—the Mediterranean and the Atlantic (Carreras et al. 2006, 2008b)—the Adriatic seems to be a foraging ground for Mediterranean loggerheads only (Giovannotti et al. 2010).

The Mediterranean Sea is severely impacted by many anthropogenic factors such as increasing exploitation of resources, use and the degradation of habitats, and different types of pollution (UNEP/MAP/BLUE PLAN 2009). The main identified threats at sea to loggerhead sea turtles in the basin include incidental capture in fishing gears, collision with boats and intentional killing (Panigada et al. 2008; Tomás et al. 2008; Casale et al. 2010; Casale 2011), which impact the overall mortality (Casale et al. 2007b, 2010) and represent a high level of threat (Wallace et al. 2011). There is growing evidence of these and other anthropogenic threats in the Adriatic: bycatch and collision with boats, debris ingestion and pollutants (Lazar and Tvrtković 1995; Affronte and Scaravelli 2001; Casale et al. 2004, 2010; Franzellitti et al. 2004; Lazar and Gračan 2011; Lazar et al. 2011b).

It is widely recognised that sea turtle conservation cannot be limited to the reproductive phase and sites, but needs measures directed to protect turtles of all stages whilst in their foraging grounds (Crouse et al. 1987; Mazaris et al. 2006). Sea turtle movements have been investigated for a long time by capture–mark–recapture with flipper tags, but such data are intrinsically unable to provide information on movement patterns between release and re-encounter events. In recent times, satellite tracking has rapidly improved our knowledge on many aspects of sea turtle movements and distribution, such as the whole range of a population including nesting and foraging grounds, migration routes, home ranges, seasonal patterns, habitat use and navigational capabilities (for an overview, see Godley et al. 2008). Adult females are the easiest class to study because they come ashore to nest, and many studies have documented the post-nesting routes followed by loggerhead females in various parts of the world (see Godley et al. 2008). The Mediterranean Sea is no exception to this, and few adults have been tracked by satellite whilst migrating from Zakynthos (Greece) to the Adriatic Sea (Zbinden et al. 2008, 2011; Hays et al. 2010b; Schofield et al. 2010). However, these adult movements are inherently affected by reproductive behaviour and cannot be assumed to provide information about the movement patterns of juveniles, which represent the bulk of the population. So far, detailed information of the spatial behaviour of loggerhead turtle juveniles foraging in the Adriatic is still lacking.

We investigated the movements of juvenile and adult loggerhead turtles foraging in the Adriatic Sea by satellite tracking, with the aim of identifying key subareas, like high-use foraging grounds and migratory corridors, assessing the temporal use of the Adriatic (all-year round, seasonal) and connections with other Mediterranean areas. Such information is fundamental to improving our understanding of sea turtle behavioural ecology through the peculiar case of a semi-closed area like the Adriatic Sea and to contributing to conservation planning in the area.

Materials and methods

In 2006 and 2007, we deployed satellite transmitters on seven loggerheads (Table 1) caught in fishing gear (turtles B, D, E and G) or found in harbours or stranded (turtles A, C and F) in the northern Adriatic Sea. They were kept in captivity in rescue centres for a period of 16–263 days (mean ± SD: 104 ± 86;

Table 1 General statistics of seven sea turtles tracked in the Adriatic Sea via satellite

Turtle	CCL (cm)	Release site	Release date	Days in captivity	Last fix date	Total tracking days	*N* day fixes	Total distance travelled (km)
A	60	Rimini (IT)	22 July 2006	90	1 June 2007	314	120	1,278
B	60	Porto Garibaldi (IT)	5 August 2006	16	12 September 2006	38	16	184
C	47	Numana (IT)	12 August 2006	151	23 September 2006	42	10	73
D	53.6	Piran (SI)	6 September 2006	17	14 November 2006	69	49	806
E	66.5	Losinj (HR)	7 September 2006	75	19 May 2007	254	60	1925
F	87	Numana (IT)	20 October 2006	117	7 January 2008	444	160	7,538
G	52	Rimini (IT)	6 November 2007	263	19 July 2008	256	100	2,949

CCL curved carapace length

Table 1). Those turtles in need of veterinary treatment were released when completely rehabilitated. Curved carapace length notch to tip was measured (CCL; Bolten 1999) and ranged from 47 to 87 cm (mean ± SD: 60.9 ± 13.2 cm; Table 1). On average, Mediterranean loggerhead turtles mature at a size larger than 70 cm CCL (Margaritoulis et al. 2003; Casale et al. 2005); therefore, it is likely that all of the tracked turtles were still immature except the largest one (turtle F), which was an adult female.

Argos-linked platform terminal transmitters (PTTs), model KiwiSat 202 (Sirtrack Ltd, New Zealand), were attached on the second vertebral carapace scute with a two-part epoxy resin (Power Fasteners, the Netherlands). The duty cycle was 3 days on from 0000 to 1200 and 3 days on from 1200 to 0000, expect for turtle A for which a continuous cycle was used.

PTT locations were collected by Argos (www.argos-system.org) and automatically downloaded by the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005). STAT also provided seafloor depth (General Bathymetric Chart of the Oceans and ETOPO2 Global 2-Minute Elevations) and sea surface temperature (SST) (NOAA Geostationary Operational Environmental Satellites, GEOS).

Valid Argos locations were categorised into six location classes (LCs) for which a recent study (Royer and Lutcavage 2008) has estimated the following order of accuracy (from higher to lower accuracy): LC 3, 2, 1, A, B and 0. Only some of the locations obtained were considered. In order to study the turtles' general movements, patterns and preferred areas, we selected only one fix per day. For days with more than one fix, the one with the highest accuracy LC was chosen. If more than one fix had this LC, the one closest to midday was selected (Zbinden et al. 2008). However, fixes of the less accurate LCs B and 0 were removed if they caused the speed between the fix and the previous or next fixes to be over 3 km h^{-1}. Such speeds were considered erroneous because they were never observed when calculating the speeds between the most accurate fixes of LCs 3, 2, 1 and A (Hays et al. 2001; Royer and Lutcavage 2008). However, only four fixes were removed following this criterion. Minimum distance travelled and minimum speed between fixes were calculated using all the filtered fixes, assuming straight-line movements between consecutive locations.

Results

The seven turtles were tracked for a period ranging from 38 to 444 days (mean ± SD: 202 ± 156), providing a total of 515 day fixes, and their minimum distance travelled ranged from 73 to 7,538 km (mean ± SD: 2,108 ± 2,597) (Table 1). Average speed for the entire travel ranged from

Table 2 Speed, depth of sea bottom and temperatures at the locations of seven loggerhead turtles tracked in the Adriatic Sea

Turtle	Speed between fixes (km h^{-1}) mean ± SD (range; *n*)	Overall speed (km d^{-1})	Depth at fixes (m) mean ± SD (range; *n*)	Fixes at depth <200 m (%)	SST at fixes (°C) mean ± SD (range; *n*)
A	0.37 ± 0.39 (0.01–1.81; 119)	4.1	26 ± 12 (3–41; 120)	100	20.1 ± 6.1 (10.1–29.0; 97)
B	0.36 ± 0.55 (0.01–1.88; 15)	4.8	10 ± 9 (2–27; 16)	100	24.8 ± 1.3 (23.3–26.9; 11)
C	0.08 ± 0.07 (0.00–0.23; 9)	1.7	19 ± 23 (5–68; 9)	100	24.8 ± 1.2 (22.5–26.1; 8)
D	0.56 ± 0.45 (0.05–2.54; 48)	11.7	50 ± 19 (5–101; 48)	100	21.0 ± 1.9 (17.5–23.7; 43)
E	0.66 ± 0.60 (0.01–2.27; 59)	7.6	99 ± 58 (2–219; 58)	91	18.4 ± 3.7 (12.4–25.5; 55)
F	0.86 ± 0.60 (0.05–2.91; 159)	17.0	714 ± 1062 (1–3669; 148)	53	19.4 ± 4.2 (15.1–29.7; 135)
G	0.77 ± 0.63 (0.03–3.00; 99)	11.5	268 ± 359 (11–1569; 100)	72	19.8 ± 5.0 (13.5–27.0; 91)

Overall speed is calculated as total distance travelled divided by total tracking days (Table 1)

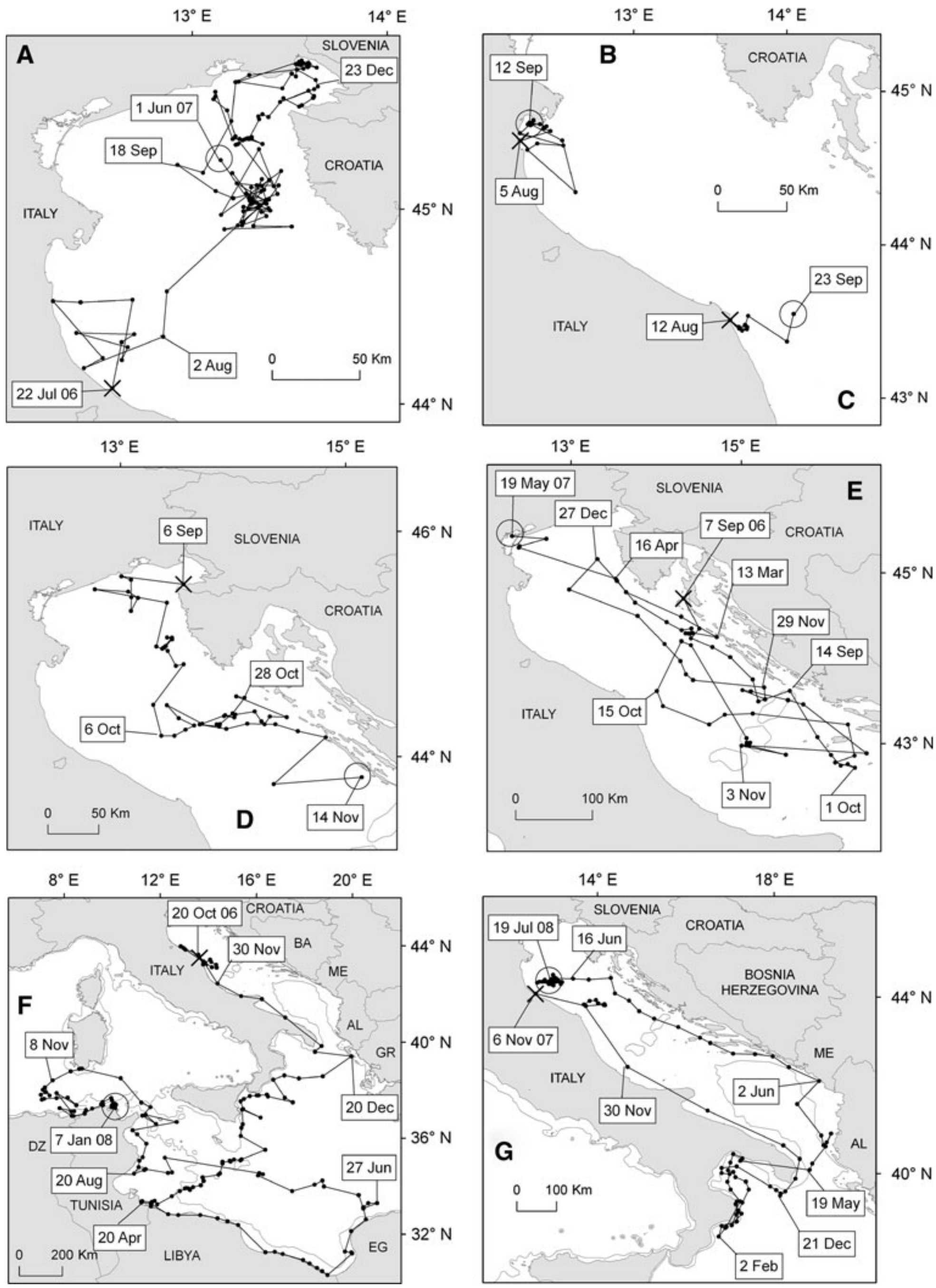

Fig. 1 Courses of seven turtles reconstructed by satellite tracking in the Adriatic and the Mediterranean Sea. *Letters* (*A*, *B*, *C*, *D*, *E*, *F* and *G*) indicate individual turtles. *Crosses* and the *circles* indicate release and last locations, respectively. The 200 m isobath is delineated. *AL* Albania, *DZ* Algeria, *BA* Bosnia; and Herzegovina, *EG* Egypt, *GR* Greece, *ME* Montenegro

1.7 to 17.0 km d^{-1}, whilst between consecutive fixes, the mean average speed was below 1 km h^{-1} for all turtles (Table 2).

Some PTTs (B, C and D) stopped transmitting much sooner than the others, but the reason is uncertain. There are several possible causes of failure such as battery exhaustion, saltwater switch failure, tag removal, animal mortality, electronic malfunction and biofouling (Hays et al. 2007). Available data from our PTTs were unable to point to a specific cause, although any mortality allowing the body to float can be excluded as well as battery exhaustion.

The tracked turtles showed a variety of movement patterns (Fig. 1). Most turtles (A, B, C, D and E) remained in the Adriatic for all the tracking period (38–314 d) and especially in the north Adriatic where they were originally found and released (A, B, C and D). Turtles B and C showed very limited movements, which were only partly due to the relatively short period of tracking (38–42 d), whilst turtles A and E wandered around the Adriatic for long periods (254–314 d) showing no directed movements towards specific destinations. The other two turtles (F and G), both released in early autumn, went out of the Adriatic and showed two other behavioural patterns. Turtle G moved southwards (30 Nov, SST <15 °C) and reached the Ionian coast of southern Italy, then came back to the northern Adriatic in the successive spring returning close to the release place where it stayed for some time before the transmissions ended. Turtle F moved southwards (30 Nov, SST <16 °C) and also left the Adriatic Sea, but it did not come back. On the contrary, its movements between different areas showed no evident patterns (e.g. seasonal migrations) in more than 1 year of tracking.

SSTs at turtle locations ranged between 10.1 and 29.7 °C (Table 2) during the tracking period (July 2006–July 2008). Not surprisingly, turtles A and F experienced the coldest and warmest temperatures, respectively. The four turtles (A–E) that remained within the Adriatic Sea (Table 2, Fig. 2) typically resided in neritic waters (<200 m in depth). Conversely, 28 % of the fixes for turtle G were received from oceanic areas (>200 m depth) in the southern Adriatic and Ionian Sea, whereas turtle F was characterised by the greatest overall speed and spent its time equally between neritic and oceanic habitats (Table 2, Fig. 2).

Discussion

We provide strong evidence of a clear migratory pattern and a strong fidelity to specific foraging areas by juvenile loggerheads in the Mediterranean. Our findings extend those reported for juvenile loggerhead turtles tracked from the Bay of Naples, one of which entered the Adriatic (Hochscheid et al. 2010). In this respect, the case of turtle G is particularly informative, since it performed seasonal migrations shuttling between two distant foraging grounds and showed fidelity to a specific north Adriatic foraging ground. Whilst its summer foraging ground (northern Adriatic) was typically neritic, the area frequented by this turtle in winter (coastal Ionian Sea) was a mix of neritic and oceanic habitats. The initial southward movements of turtle G were directed and seem to have a clear migratory nature induced by temperature, having been performed in the period of cooling waters in the north Adriatic. The same pattern was shown by the adult turtle F, and both moved southwards at temperatures <16 °C. Seasonal migrations have been observed in some loggerhead population and areas, like the north-western Atlantic, where turtles migrate to remain in waters >17 °C (Musick and Limpus 1997; Hawkes et al. 2011). This was also the explanation for

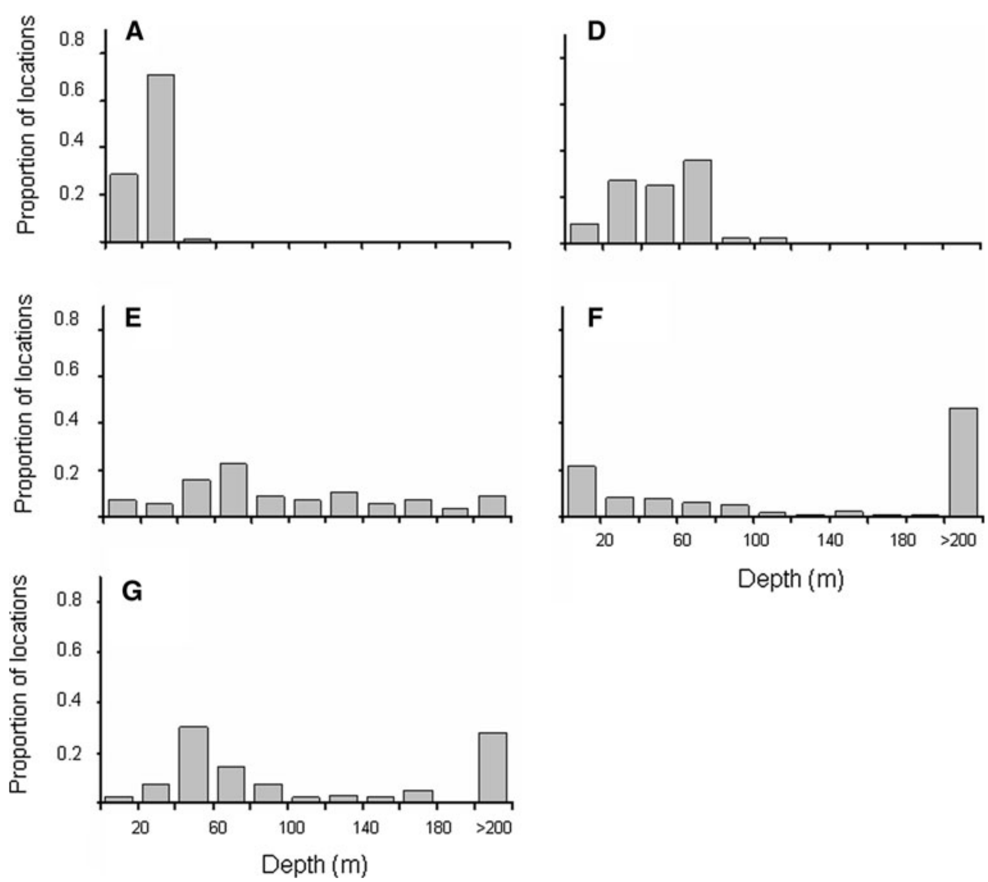

Fig. 2 Frequency distribution of depth at the location of five loggerhead turtles (a, d, e, f and g) (n = 474)

those adult females observed to leave the north Adriatic in the cold period (Zbinden et al. 2011) as well as for lower turtle occurrence during winter in the two northernmost areas of the Mediterranean—the north Adriatic (Lazar et al. 2003) and the Ligurian Sea (Lauriano et al. 2011)—where winter temperatures are <13 °C. Although turtle D was tracked for a relatively short period, it showed a tendency to move southward.

However, there is evidence from bycatch (Casale et al. 2004) and stranding records (Casale et al. 2010; Scaravelli, unpubl data) that at least some loggerhead turtles frequent the wider north Adriatic area also in winter. The case of turtle A expands the winter occurrence of turtles in the Adriatic to the northernmost part (Gulf of Trieste) that is the coldest of the Mediterranean and its low winter temperatures (below 11–12 °C) were thought to induce turtles to leave this area and migrate to the south (Lazar et al. 2003). Actually, turtle A had a prolonged permanence in this area with SSTs as low as 10.1 °C. The capacity of loggerhead turtles to maintain some level of activity in comparable or somewhat higher thermal conditions is known (min 11.8 °C; Hochscheid et al. 2007). In summary, our present results further support the behavioural plasticity of the species recently reported for adults (e.g. Hatase et al. 2002; Hawkes et al. 2006) by showing different behaviours such as permanence and migration observed in juvenile turtles frequenting the same area.

Turtle F was an adult and provides evidence of a peculiar behaviour. Since it was not localised at a specific coastal place during the nesting season (June–August; Margaritoulis 2005), we conclude that it was in a non-breeding year (Broderick et al. 2003; Hays et al. 2010b) and its rookery remain unknown. Although adult females in the Mediterranean are known to show fidelity to specific neritic foraging grounds (Broderick et al. 2007; Zbinden et al. 2011), turtle F showed no sign of fidelity to any area, in the Adriatic or elsewhere, in neritic or oceanic zones, despite having been tracked for more than 1 year. The post-nesting track of one adult female from Greece (Zbinden et al. 2008), although only 6 months long, suggests a pattern similar to turtle F, with an initial movement towards the north Adriatic followed by a return to more southern waters with an apparent wandering behaviour. Similar wandering movements different from relatively small home ranges were also observed in adult males (Schofield et al. 2010). However, most satellite tracking data on adult females nesting at Zakynthos showed a clear-cut separation between foraging areas, with some turtles migrating to and then residing in neritic habitats either in the Adriatic Sea or at the continental shelf off the Tunisian and Libyan coasts (Zbinden et al. 2008, 2011). Turtle F provides an additional pattern, since it foraged in both areas in different years: it was captured in summer 2007 in the Adriatic and then it remained at the African continental shelf for months in 2008. Its track therefore provides compelling evidence of a connection between two most important foraging grounds for loggerhead turtles in the Mediterranean: the Adriatic Sea, frequented by loggerheads from at least Greece, Turkey and Cyprus (Lazar et al. 2004b; Giovannotti et al. 2010) and the continental shelf off Tunisia, frequented by loggerheads from most or all Mediterranean rookeries as well as by loggerheads of Atlantic origin (Casale et al. 2008b).

A possible explanation for turtle F movements is the ‘nomad’ behavioural pattern, originally suggested for large juveniles in the Mediterranean, characterised by continuous movements among distant areas with no evident settlement and residence (Casale et al. 2007a). Different movement patterns of adult loggerheads belonging to the same population have recently been reported from outside the Mediterranean, where some adult turtles have been found to frequent oceanic feeding grounds after the nesting season, foraging on epipelagic prey (Hatase et al. 2002; Hawkes et al. 2006; Hatase et al. 2010; Rees et al. 2010). In this respect, turtle F provides a further example of the occurrence of this alternative foraging strategy in loggerheads, since it spent a considerable amount of time in oceanic waters. In other cases (Hatase et al. 2002; Hawkes et al. 2006), such a behavioural polymorphism was related to the size of the animals, with larger and smaller turtles foraging in neritic and oceanic waters, respectively. However, this does not seem to apply to turtle F, which was well above the average size for Mediterranean adult females (Margaritoulis et al. 2003). On the basis of a previous study on juveniles (Casale et al. 2007a), this behavioural polymorphism would already begin at an early age, with some turtles never settling to a specific foraging area as they grow and become adult.

Identifying highly frequented off-shore areas is a key priority for sea turtle conservation (Hamann et al. 2010). For instance, if fishing effort or boat traffic, two of the major threats for sea turtles in the Mediterranean (Casale et al. 2010; Casale 2011), could be adequately managed in an area highly frequented by turtles or displaced to less frequented areas, the overall anthropogenic turtle mortality would decrease. In this study, the few cases of turtles remaining in relatively small areas at least for some time (turtles A, B and G) did not overlap. Therefore, although highly frequented areas might exist, a larger sample size is required to investigate this aspect. On a broader scale, the present tracks indicate that the eastern part of the Adriatic is more frequented by juvenile sea turtles than the western one (turtles A, D and E), supporting what was previously suggested on the basis of catch rates by fishing gear (Casale et al. 2004). Accordingly, diet analyses show that loggerhead turtles ranging from 25.0 to 85.4 cm CCL actively feed on benthic prey in the eastern Adriatic (Lazar et al. 2011a).

Migratory pathways represent additional critical areas for endangered species. The present tracks show two cases of southward directional movements in autumn, from the north Adriatic to the south Adriatic and to the Ionian Sea along the Adriatic western coast (turtles F and G) and one case of northward movement in spring along the eastern coast (turtle G), a finding that fits with the general counter-clockwise current pattern of the Adriatic (Zavatarelli and Pinardi 2003). Coastal pathways in the Adriatic have also been reported for adults breeding in Greece (Schofield et al. 2010; Zbinden et al. 2011). Moreover, the movements of turtle F highlight the importance of the North African coast as a pathway for loggerhead turtles in the Mediterranean, in accordance with the tracks of adult females nesting in Cyprus (Broderick et al. 2007).

The Adriatic is one of the two main foraging areas for adult loggerhead turtles from the Greek nesting site of Zakynthos (Lazar et al. 2004b; Zbinden et al. 2008, 2011; Hays et al. 2010a; Schofield et al. 2010) but is also frequented by turtles from rookeries in Turkey and Cyprus (Lazar et al. 2004b; Giovannotti et al. 2010). Present findings indicate that not only the adults but also the juveniles likely arriving from these rookeries are permanent or at least seasonal residents of the Adriatic. These results add to a growing body of evidence, such as models of hatchling dispersal (Hays et al. 2010a), stranding (Casale et al. 2010) and mark–recapture data (Casale et al. 2007a), corroborating the hypothesis that part of the Greek population spends their entire life in different habitats of the relatively small north Ionian/Adriatic area (Casale et al. 2007a). This further supports the value of a recently proposed management strategy aimed to reduce the fishery-related mortality in the Ionian–Adriatic area (Lazar et al. 2004b).

Loggerheads appear to distribute in a non-uniform manner in the Adriatic Sea and future studies should be aimed to identify the highest density neritic areas, since they would represent priority areas for focusing conservation measures. Satellite tracking is rapidly improving our knowledge of turtle behavioural ecology, even with limits on the number of tracked turtles. Although most sea turtle studies are based around breeding adults and the nesting beach, studies at sea, like the present one and others (e.g. Revelles et al. 2007; Cardona et al. 2009), can reveal wider patterns and unveil the movements and distribution of juveniles, which remain the least studied age class, the 'under-represented majority' (Godley et al. 2008).

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