



Shelf life: neritic habitat use of a turtle population highly threatened by fisheries

Robin T. E. Snape^{1,2*}, Annette C. Broderick¹, Burak A. Çiçek³,
Wayne J. Fuller^{2,4}, Fiona Glen², Kimberley Stokes¹ and Brendan J. Godley¹

¹Marine Turtle Research Group, Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK, ²Society for Protection of Turtles, PK.65, Kyrenia, North Cyprus, Mersin 10, Turkey, ³Underwater Research and Imaging Centre, Biological Sciences Department, Eastern Mediterranean University, Famagusta, North Cyprus, Mersin 10, Turkey, ⁴Faculty of Veterinary Medicine, Near East University, North Cyprus, Mersin 10, Turkey

ABSTRACT

Aim It is difficult to mitigate threats to marine vertebrates until their habitat use is understood. We report on a decade of satellite tracking loggerhead turtles (*Caretta caretta*) from an important nesting site to determine priority habitats for their protection in a region where they are known to be heavily impacted by fisheries.

Location Cyprus, Eastern Mediterranean.

Method We tracked 27 adult female loggerheads between 2001 and 2012 from North Cyprus nesting beaches. To eliminate potential biases, we included females nesting on all coasts of our study area, at different periods of the nesting season and from a range of size classes.

Results Foraging sites were distributed over the continental shelf of Cyprus, the Levant and North Africa, up to a maximum distance of 2100 km from nesting sites. Foraging sites were clustered in (1) near-shore waters of Cyprus and Syria, (2) offshore waters of Egypt and (3) offshore and near-shore regions of Libya and Tunisia. The North Cyprus and west Egypt/east Libyan coasts are important areas for loggerhead turtles during migration. Movement patterns within foraging sites strongly suggest benthic feeding in discrete areas. Early nesters visited other rookeries in Turkey, Syria and Israel where they likely laid further clutches. Tracking suggests minimum annual mortality of 11%, comparable to other fishery-impacted loggerhead populations.

Main conclusions This work further highlights the importance of neritic habitats of Libya and Tunisia as areas likely used by loggerhead turtles from many of the Mediterranean rookeries and where the threat of fisheries bycatch is high. Our tracking data also suggest that anthropogenic mortalities may have occurred in North Cyprus, Syria and Egypt; all within near-shore marine areas where small-scale fisheries operate. Protection of this species across many geopolitical units is a major challenge and documenting their distribution is an important first step.

Keywords

bycatch, *Caretta*, conservation, distribution, fisher, foraging, migration, mortality, telemetry, threat.

*Correspondence: Robin T. E. Snape, Marine Turtle Research Group, Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK. E-mail: rtes201@exeter.ac.uk

INTRODUCTION

Many marine vertebrate species have evolved to be long-lived, a strategy which can render their populations particularly sensitive to anthropogenic mortality (Lewison *et al.*, 2004). Sea turtles, sharks, seabirds and marine mammals have been particularly impacted by man, mostly attributable

to direct harvesting and/or fisheries bycatch, radically reducing many populations (Spotila *et al.*, 2000; Clarke *et al.*, 2013; Maxwell *et al.*, 2013; Paleczny *et al.*, 2015). If these anthropogenic threats are to be mitigated, the distribution of vulnerable populations must be understood. Aerial and ship-based surveys can be used to infer the relative abundance of species in specific areas of interest (Lauriano *et al.*, 2011;

Hammond *et al.*, 2013; Hodgson *et al.*, 2013). Large marine vertebrates, however, are usually highly mobile, exploiting habitats across wide, diverse and remote areas (Bowen *et al.*, 1995; Robinson *et al.*, 2009). For such taxa, studies using animal-borne tracking devices can yield ground-breaking insights into the wider ecology of the study species (Rodhouse *et al.*, 1996; Croxall *et al.*, 2005; James *et al.*, 2006).

Sea turtles have been the subject of significant satellite tracking effort (Godley *et al.*, 2008). A common finding is that, even among individuals of the same population, patterns of habitat use are heterogeneous (Hawkes *et al.*, 2006; Rees *et al.*, 2010a). Sample sizes should ideally be large enough to capture such variation but are often constrained by the high cost of devices and satellite services. The results of investment in programmes of satellite telemetry over periods of many years, where cumulative costs are met in stages, are increasingly yielding dividends (Tucker, 2010; Griffin *et al.*, 2013; Pikesley *et al.*, 2013; Schofield *et al.*, 2013).

The Mediterranean loggerhead turtle population can be regarded as functionally independent from other Atlantic populations (Laurent *et al.*, 1998; Carreras *et al.*, 2011) and has experienced declines in response to historical harvesting, fisheries interactions and coastal development (Casale & Margaritoulis, 2010). As such, Mediterranean loggerhead turtles have been described as a Regional Management Unit that is at low risk but under high threat (Wallace *et al.*, 2011). The IUCN (International Union for Conservation of Nature) recently classified the Mediterranean loggerhead subpopulation as 'Least Concern' on the basis of an overall increasing estimated population, a relatively large distribution and a relatively large estimated population. This status, however, is entirely conservation dependant, as the increasing estimated population trend is the product of decades of intensive conservation efforts at nest sites and could be reversed should these efforts cease (Casale, 2015).

Fisheries bycatch is the greatest threat to loggerhead turtles globally, and bycatch rates in the Mediterranean are among the highest in the world (Wallace *et al.*, 2010, 2011; Casale, 2011). Genetic analyses in the west and central Mediterranean show that pelagic Mediterranean habitats are shared with loggerheads from populations nesting in the western Atlantic (Laurent *et al.*, 1998; Carreras *et al.*, 2006). However, bycatch samples from neritic fisheries throughout the basin rarely include western Atlantic haplotypes, suggesting that loggerheads from these distant stocks leave the Mediterranean, prior to a developmental shift to neritic habitats (Revelles *et al.*, 2007; Carreras *et al.*, 2011; Garofalo *et al.*, 2013). Bycatch in neritic areas of the Mediterranean therefore predominantly impacts Mediterranean stocks; specifically, larger post-pelagic animals that are of higher reproductive value than pelagic juveniles (Wallace *et al.*, 2008; Casale, 2011; Snape *et al.*, 2013). Management of this bycatch is therefore a priority, and an understanding of the distribution of turtles is a clear prerequisite.

Studies published to date to investigate the habitat use of female post-breeding Mediterranean loggerheads have

focused on two of the main rookeries in Greece and Cyprus, whose coastlines support approximately 48% and 9% of nesting for this population, respectively (Casale & Margaritoulis, 2010). Key findings of these studies are that (1) turtles show fidelity both to foraging sites and to migratory routes between breeding and foraging sites, (2) nearly all forage in neritic waters, aggregating in areas with wide availability of continental shelf, and (3) most turtles reside at the same foraging site for long periods (Godley *et al.*, 2003; Broderick *et al.*, 2007; Zbinden *et al.*, 2011; Schofield *et al.*, 2013). Here, we aimed to provide a more holistic assessment of migratory corridors and key foraging areas, by extending our North Cyprus study (Godley *et al.*, 2003; Broderick *et al.*, 2007), incorporating a much larger sample size and deploying from a range of sites over the entire duration of the nesting season.

METHODS

Twenty-seven adult female loggerhead turtles were tracked after nesting in North Cyprus (coastline of approximately 325 km) between 2001 and 2012 (Table 1). The results of 10 of these deployments have previously been described by Godley *et al.* (2003) and Broderick *et al.* (2007).

As biases within and among seasons and across size classes are capable of producing dramatically misleading results (Hawkes *et al.*, 2006; Rees *et al.*, 2010a; Witt *et al.*, 2011), our deployments were made over several years, were spread across nearly every week of the nesting season and across most size classes (Fig. 1). To reduce potential bias associated with nesting sites, turtles were tracked from nesting sites on every coast (Fig. 2a insert). PTTs were attached according to the protocol outlined by Godley *et al.* (2002). A variety of PTT models were used during the 11-year deployment period (Table 1). Prior to device attachment, minimum curved carapace length (CCL_{min}; Bolten, 1999) was recorded (Table 1).

Location data were handled using Satellite Tracking Analysis Tool (STAT; Coyne & Godley, 2005). To eliminate erroneous data, location classes 0 (error >1.5 km) and Z (failed Argos plausibility tests) and those inferring speeds of >5 km h⁻¹ (greater than expected swimming speeds for marine turtles; Witt *et al.*, 2010) were removed. We visually inferred broad behavioural patterns, with all turtles undertaking clear post-nesting migrations to neritic foraging sites where they took up residency in discrete areas; a common strategy for loggerhead turtles, particularly in the Mediterranean (Luschi & Casale, 2014; minimum, this study: 27 days). Where turtles shuttled between more than one discrete area (centroids >10 km distant), data were split and analysed separately.

To visualize the shape and approximate magnitude of core areas of habitat use, the 'Kernel Density Estimator' command of Geospatial Modelling Environment (GME) was used to produce kernels for filtered foraging site data. As size of kernels can be influenced by many factors other than the

Table 1 Summary of transmitter deployments included in this study. Data from 10 turtles were previously published by Godley *et al.* (2003; turtles C and H) and Broderick *et al.* (2007; turtles A, C, G, H, L, M, O, R, V and X). Turtles C, R and X were tracked from more than one nesting season. For turtles C and X, the first migration track and the foraging site with greatest number of foraging days were plotted in Figs. 2 and 3, respectively. Deployment sites: Alagadi: 35°20'N, 33°29'E; Iskele: 35°16'N, 33°55'E; Akdeniz: 35°20'N, 32°56'E. Estimated depth at foraging sites is the median estimated depth of the filtered Argos locations that were used to generate foraging site kernels (bathymetry data sourced at GEBCO global topographic dataset with one-minute (1') spatial resolution (<http://www.gebco.net/>)).

Turtle ID	PTT	Manufacturer	Model	Deploy site	Deploy date	CCLmin (cm)	Tracking days	Foraging site EEZ	Foraging days	Number of sites used	For multiple sites (site name:total visits,total days)	Estimated depth (m) at foraging site(s)
A	15414	Telonics	ST6	Alagadi	4-Jul-02	72	404	Cyprus	359	1		7.4
B	118185	Wildlife Computers	SPOT	Iskele	31-May-12	65	352	Cyprus	913	1		53.2
C	29358	Telonics	ST14	Alagadi	11-Jul-01	71	81	Cyprus	58	1		-
C	29050	Telonics	ST18	Alagadi	14-Jun-03	73	1405	Cyprus	1368	1		78.4
D	52813	Sirtrack	K2G	Tatlisu	17-Jun-11	71	1303	Cyprus	1270	2	D1:14,852;D2:13,418	8.6
E	77171	SMRU	SRD L	Alagadi	16-Jul-08	66	708	Cyprus	683	2	E1:3,468;E2:2,215	29.5
F	52816	Sirtrack	K2G	Akdeniz	23-Jun-11	73	393	Syria	370	1		5.5
G	29034	Telonics	ST18	Alagadi	21-Jul-03	77	628	Syria	604	3	G1:1,63;G2:2,296;G3:3,245	17.9
H	29359	Telonics	ST14	Alagadi	13-Jun-01	73	59	Syria	38	1		121.0
I	77172	SMRU	SRD L	Alagadi	2-Jul-09	64	268	Syria	248	2	I1:1,85;I2:1,163	89.3
J	68557	SMRU	SRD L	Alagadi	8-Jun-07	85	260	Lebanon	190	1		8.0
K	52817	Sirtrack	K2G	Iskele	1-Jun-12	74	67	Egypt	27	1		2.1
L	15340	Telonics	ST6	Alagadi	5-Jun-02	71	226	Egypt	195	1		95.0
M	57389	Sirtrack	101	Alagadi	1-Jul-05	76	135	Egypt	80	1		99.9
N	52819	Sirtrack	K2G	Akdeniz	5-Jun-11	73	440	Egypt	367	1		66.7
O	4406	Telonics	ST14	Alagadi	3-Aug-02	69	86	Egypt	71	1		86.4
P	43755	Sirtrack	F4	Iskele	5-Jun-12	68	174	Libya	99	1		72.8
Q	68561	SMRU	SRD L	Alagadi	20-Jun-07	67	166	Libya	102	1		86.2
R	4407	Telonics	ST14	Alagadi	17-Jul-02	73	392	Libya	320	2	R1:2,206;R2:1,114	52.5
R	29049	Telonics	ST18	Alagadi	5-Jun-04	75	70	-	-	-		-
S	52815	Sirtrack	K2G	Iskele	1-Jun-12	75	351	Libya	246	1		96.5
T	53184	SMRU	SRD L	Alagadi	5-Jun-06	65	389	Libya	262	2	T1:3,110;T2:2,152	55.1
U	53182	SMRU	SRD L	Alagadi	21-Jun-06	77	350	Tunisia	257	1		52.6
V	4206	SMRU	SRD L	Alagadi	4-Jul-02	69	139	Tunisia	72	1		19.7
W	118184	Wildlife Computers	SPOT	Iskele	1-Jun-12	80	194	Tunisia	53	1		5.0
X	57384	Sirtrack	101	Alagadi	7-Jun-05	74	176	Tunisia	37	1		-
X	4242	SMRU	SRD L	Alagadi	8-Jul-02	74	422	Tunisia	341	1	X1:2,165;X2:1,176	7.2
Y	34214	SMRU	SRD L	Alagadi	30-Jun-06	78	63	-	-	-		-
Z	57391	Sirtrack	101	Alagadi	24-Jun-05	82	6	-	-	-		-
AA	52815	Sirtrack	K2G	Tatlisu	10-Jun-11	73	34	-	-	-		-

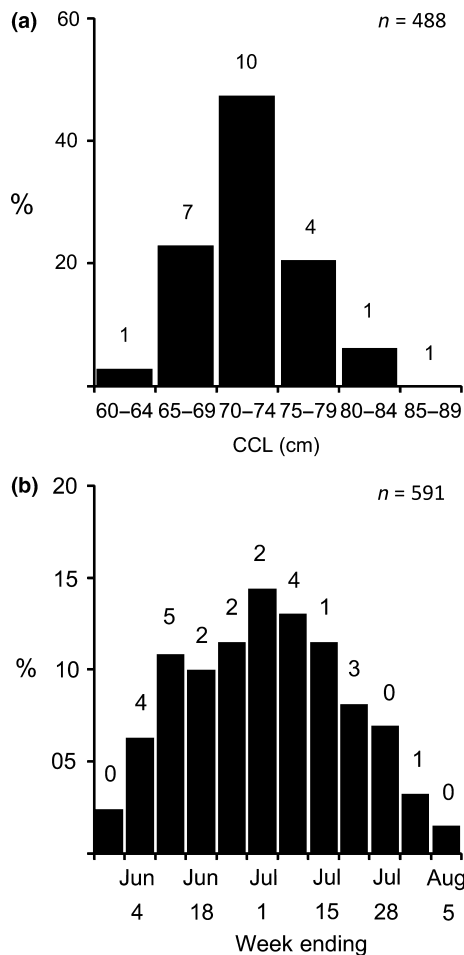


Figure 1 Percentage frequency histograms for (a) size (minimum curved carapace length) and (b) temporal distribution of nesting, of adult female loggerhead turtles on Alagadi study beach, North Cyprus. Numbers above bars represent the number individual nesting females of each bin that were tracked to foraging sites during this study.

horizontal habitat use of the study animal (Witt *et al.*, 2010), we did not seek to over-interpret and generate precise home range magnitude. We trialled a range of bandwidth levels and chose 0.0003, which we felt best described the shape of our data plots. The GME 'Isopleth' command was used to map isopleths within kernels of 20% and 50% of the total data distribution to represent the shape of core foraging areas. Where turtles occupied multiple subsites, the number of days spent within and the total number of visits to each site were compiled (Table 1).

To contextualize the threat of fisheries bycatch to study turtles, we used available fisheries bycatch information (a comprehensive review by Casale, 2011) for the countries hosting foraging of >1 study turtle.

Device terminations were attributed to the mortality of a study turtle when preceded directly by: (1) a sudden increase in the rate of messages received from devices, indicating that the device was no longer submerged, and (2) movement

away from foraging sites, indicating a deviation from expected spatial habitat use (see Hays *et al.*, 2003; Snoddy & Southwood Williard, 2010). An approximate annual mortality rate was calculated after Hays *et al.* (2003).

RESULTS

Body size of turtles tracked to foraging sites ranged from 64 to 85 cm CCLmin (mean \pm SD: 72.1 ± 4.84 cm; Table 1, Fig. 1). This is reflective of the size range previously reported by Broderick & Godley (1996) for this rookery of mean: 73.4 cm (range: 65–86.5 cm). Of the 27 study turtles, 24 individuals reached foraging sites where they remained for 27 days or more (Table 1, Fig. 2).

Interesting movements and post-nesting migrations

On leaving Cyprus, turtles took 6–86 days to reach foraging sites (mean \pm SE: 32 ± 5 days). Twenty-one of the 24 turtles tracked to foraging sites followed relatively direct trajectories during their post-nesting migrations (Fig. 2a). Three turtles (12.5%; turtles B, J and P; Fig. 2b–d) visited the coastlines of other countries during the nesting season. Turtle J was equipped with a transmitter model which logged wet and dry periods through a salt-water switch. This device recorded and transmitted data for haul-outs periods on the Turkish coast (Fig. 2b). These periods were suggestive of nesting with internesting intervals of 17 and 12 days, consistent with internesting interval ranges recorded for loggerheads in Cyprus (Broderick *et al.*, 2002). For the other two turtles of this group, we plotted likely nesting events according to clustering of location data coinciding temporally with expected nesting (Broderick & Godley, 1996) and spatially with known nesting sites (Casale & Margaritoulis, 2010; Fig. 2c–d).

During open sea crossings, routes of individual turtles were relatively dispersed, but important coastal migration routes were determined along the coasts of Cyprus (including the British Overseas Territory Sovereign Base Area (SBA) Dhekelia) and along the coast of western Egypt and Libya (Fig. 2e).

Foraging sites

Once at foraging sites, the depth of water and patterns of movement were suggestive of benthic feeding (Hawkes *et al.*, 2006), with some (7 of 24) turtles shuttling between two or three subsites greater than 10 km apart (Fig. 3, See Figure S1 in Supporting Information). In total, 32 foraging sites were mapped for durations ranging from 27 to 1405 days (Table 1). The median depth at locations for filtered Argos data at foraging sites ranged between 2 and 121 m (Table 1). Eighty-three percentage of turtles foraged in three main regions: (1) close to deployment sites in Cyprus (including British SBA Akrotiri) and Syria ($n = 9$; 38%; Fig. 3a), (2) at medium distance from deployment sites off Egypt ($n = 5$;

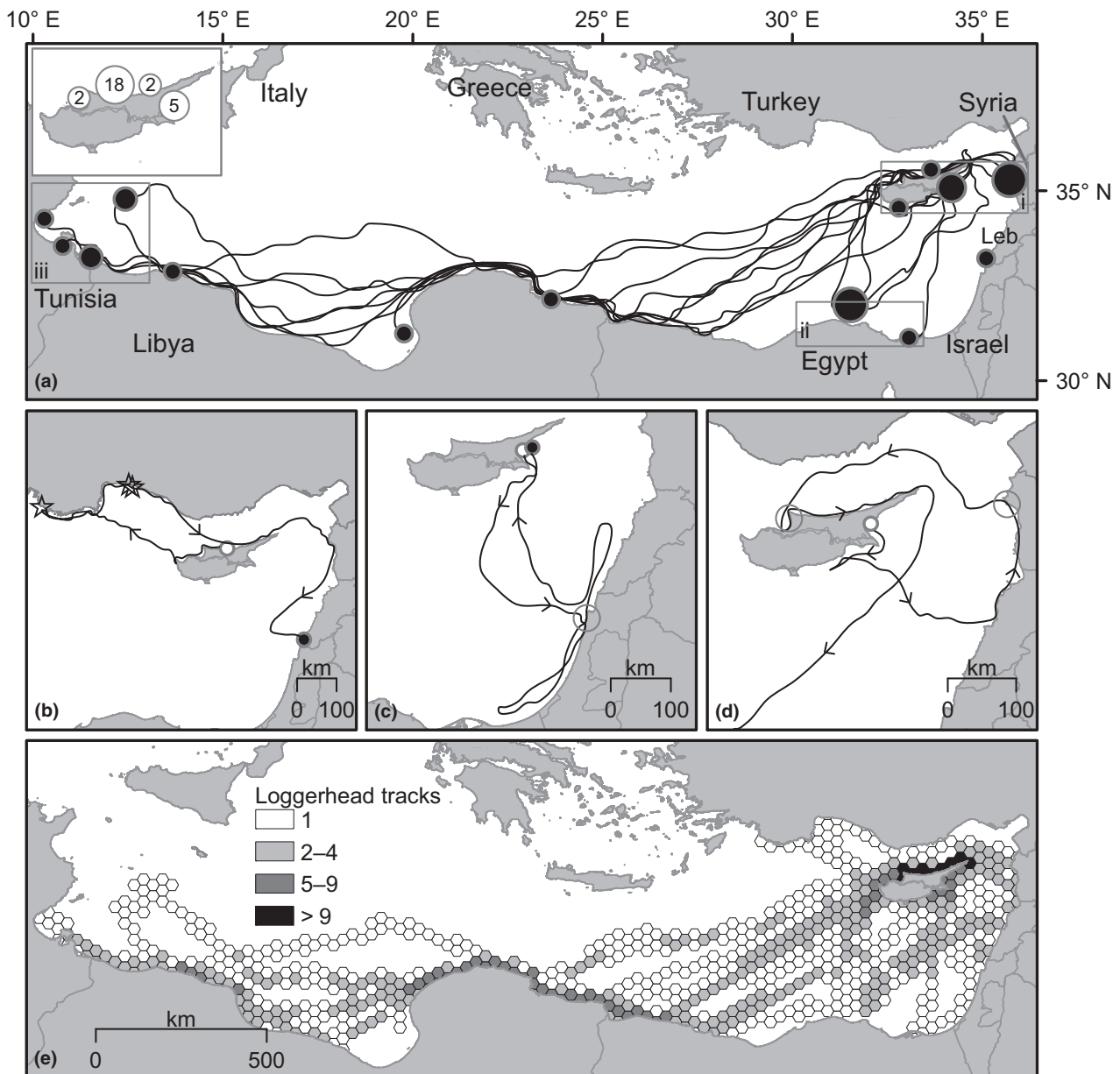


Figure 2 (a) The routes taken by turtles that made post-nesting migrations directly from North Cyprus (see insert box for deployment sites) to foraging sites and distribution of foraging sites. Black circles are scaled to the number of individuals residing in each area (1–4). Boxes i to iii indicate areas mapped in detail in Fig. 3. (b) The route taken by turtle J. Open star = sites where onboard sensors detected haul-outs in Turkey. (c) The route taken by turtle B. Open circle = inferred nest site in Israel. (d) The route taken by turtle P. Open circle = inferred nest site in Syria and on the West coast of Cyprus. (e) Migratory corridor density map of migrations to foraging sites ($n = 24$).

21%; Fig. 3b), and (3) far from deployment sites along the western Libyan and the eastern Tunisian shelf areas ($n = 6$; 25%; Fig. 3c). The remaining 17% were distributed diffusely across Libya ($n = 3$) and one individual foraged in Lebanon (see Fig. S1).

Mortalities

Argos data from turtles F and K suggest that these individuals were caught at their foraging sites in depths of the order of 5 and 2 metres, respectively (Fig. 4, Table 1). The carcass

of turtle AA was returned to us in North Cyprus 35 days post-deployment. These three deaths suggest an annual mortality rate of 0.11 (annual survival probability of 0.89) for our 9741 tracking days (Hays *et al.*, 2003).

DISCUSSION

We present insights that collectively represent a significant step towards a holistic understanding of the habitat requirements of adult Mediterranean loggerhead turtles. These data will be of great value in targeting marine turtle–fisheries interaction

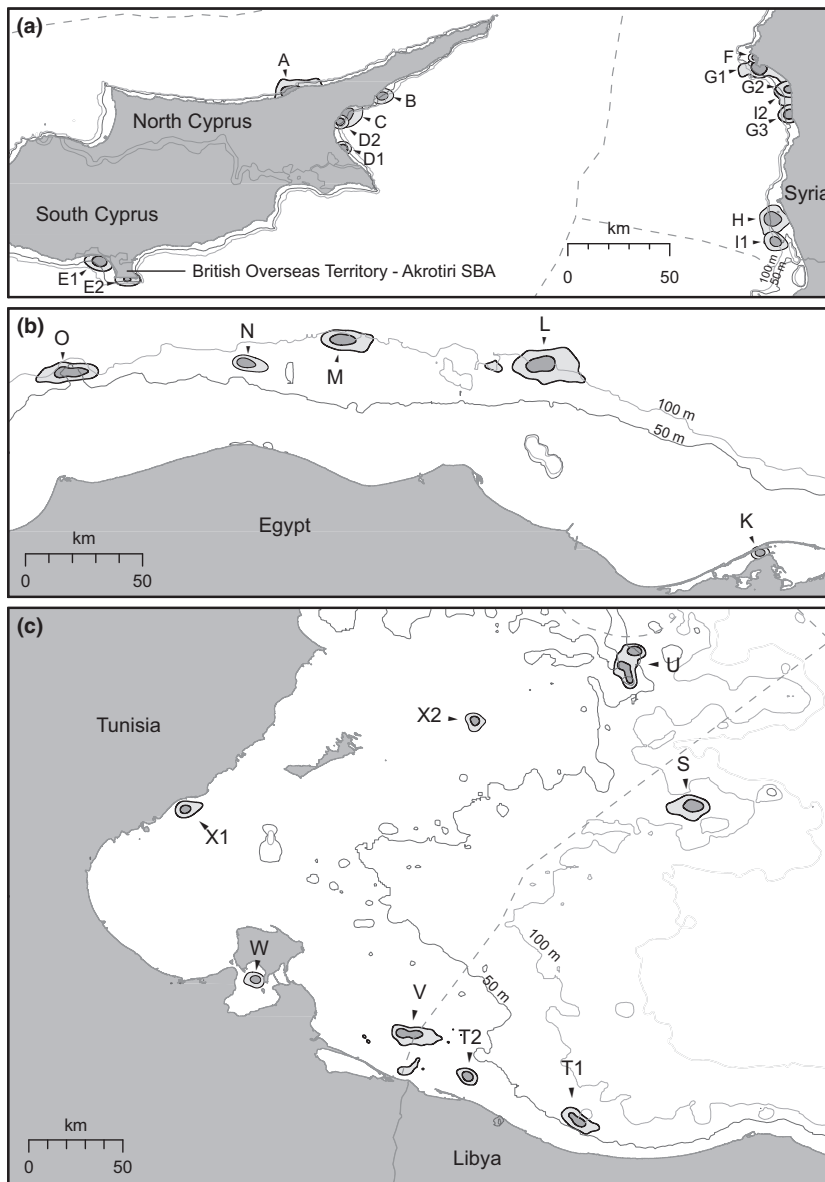


Figure 3 Twenty percent (dark grey) and 50% (light grey) data distribution isopleths produced from kernelled filtered satellite telemetry data for the main foraging sites concentrated in (a) Cyprus and Syria, (b) Egypt and (c) West Libya, the Tunisian coast and shelf. Letters represent individual turtles (Table 1) and their subsites (where numbered). Dotted line indicates Exclusive Economic Zone.

studies that are required in order to develop strategies to reduce the threat of fisheries. Our work also provides the evidence of significant international movement of females among nesting sites of this population, which will have ramifications for the study of genetic structure, design of monitoring strategies and generation of population estimates.

Life history

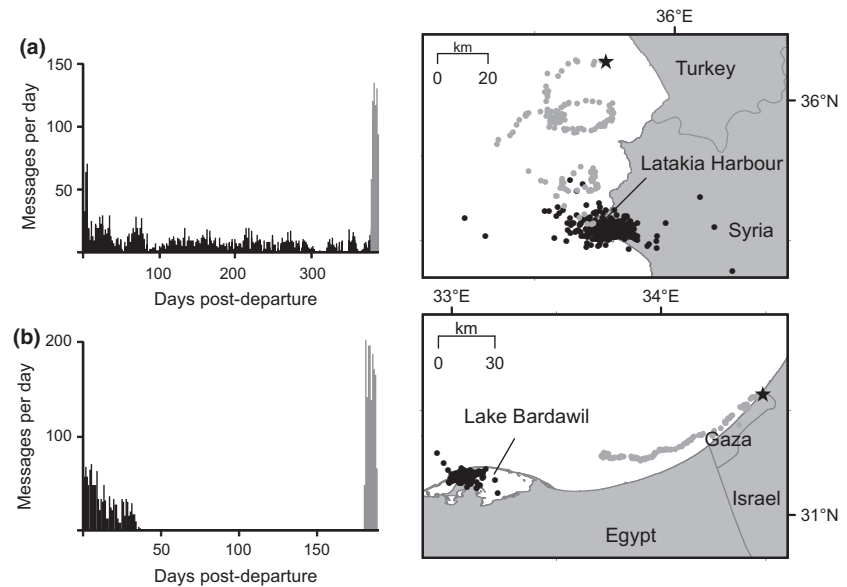
As is the case for all Mediterranean nesting females tracked to date (Luschi & Casale, 2014), turtles all appeared to be neritic foragers, making relatively direct migrations to continental shelf sites after nesting. This is despite the fact that we specifically included small individuals that have been shown to exhibit pelagic foraging in other populations (Hatase *et al.*, 2002; Hawkes *et al.*, 2006). None made marked seasonal migrations between foraging sites to avoid winter temperature extremes,

which contrasts with conspecifics using the Adriatic region of the Mediterranean (Schofield *et al.*, 2013).

Migration corridors and foraging sites

Adult loggerhead turtle densities will be elevated in the migration corridors we describe here off Cyprus, western Egypt and eastern Libya during the post-nesting migration period in July and August. These overlap significantly with those of green turtles (*Chelonia mydas*) in the region (Stokes *et al.*, 2015). Previously unreported foraging sites for this rookery were revealed on the Tunisian/Libyan shelf area, scattered along the Libyan coast, at Lake Bardawil, Egypt, off Lebanon and British Sovereign Base Area Akrotiri on Cyprus. The larger sample size here also emphasizes the importance of foraging areas previously published by Broderick *et al.* (2007).

Figure 4 Bar plot showing the number of uplinks received daily by Argos during post-nesting movements (left) and maps showing location data (Location classes 0 and Z and speeds $>5 \text{ km h}^{-1}$ removed) received after turtles reached foraging sites (right) for (a) turtle F and (b) turtle K, both of which likely died. Black stacks = data received before the turtle left its foraging site. Grey stacks = data received after the turtle left its foraging site. These stack colours correspond to black and grey positional data points. Black star denotes the last received location.



The most important foraging areas for Mediterranean loggerheads are now understood to be in neritic waters of the Adriatic, on the Tunisian/Libyan shelf, off the Nile Delta in Egypt, in Cyprus and in Syria. This broad and diffuse distribution poses a challenge to managing their conservation. Densities appear to be higher closer to nest sites in Cyprus, but one must consider that loggerheads from other rookeries will also be occupying the North African Coast and the Levant. More than a quarter of turtles tracked in this study used the Tunisian/Libyan shelf shared by a large proportion of turtles tracked from the Greek rookeries (Schofield *et al.*, 2013; Zbinden *et al.*, 2011). Nesting females subject to flipper tagging in Greece have been recovered in eastern Libya (1), Egypt (1), Israel (3) and Cyprus (2); Margaritoulis, 1988; Margaritoulis & Rees, 2011; D. Margaritoulis *pers. comm.*

The observed distribution of foraging sites may well be a product of a trade-off between the availability of suitable shelf habitat and the energetic costs of migrations. A pattern observed in our study in common with other loggerhead studies (Rees *et al.*, 2010a; Schofield *et al.*, 2010; Hawkes *et al.*, 2011) was that foraging sites were generally larger in turtles residing offshore (considered here to be where the 20% isopleth of the foraging site lies $>10 \text{ km}$ from land) and in deeper water than those on the coast. Habitat utilization in harbours and embayments was more discrete, clearly being restricted by physical boundaries. The fifty percentage core utility areas appear to be of a similar magnitude as those proposed for Mediterranean loggerheads by Schofield *et al.* (2010) of tens to hundreds of square kilometres.

Multiple-country nesting

Loggerhead females laying a single clutch in Cyprus have previously been shown to have low nest site fidelity (Broderick *et al.*, 2002). We confirm that these single clutch females

were indeed likely to be subsequently nesting elsewhere. Loggerheads are known to exhibit relatively low nest site fidelity in comparison with other species (Hays *et al.*, 1991; Tucker, 2010), and the use of multiple breeding sites by male loggerheads in the Mediterranean has also been suggested (Casale *et al.*, 2013). However, this is the first time that nesting events hundreds of kilometres apart and among multiple geopolitical units have been documented for Mediterranean loggerheads. Our estimate of 12.5% multiple-country nesting could be considered conservative, as all turtles which exhibited this behaviour were tracked from early in the season, suggesting that some of those turtles tracked later may have previously nested elsewhere. These findings challenge the accuracy of published loggerhead clutch frequencies that are based on tag returns at monitored nesting sites, and in turn, current population estimates based on reproductive outputs extrapolated to basin-wide nest counts (Broderick *et al.*, 2002; Pfaller *et al.*, 2013). These results should also be considered when planning the temporal spread of genetic sampling for haplotype analyses and further tracking studies of nesting females.

Fisheries threats

Of the main countries which host foraging adult loggerheads (current study and reviewed by Luschi & Casale (2014)), Tunisia stands out as being associated with the greatest number of turtle deaths in fisheries, with at least 5600 deaths per year occurring predominantly in set nets and bottom trawls (see Fig. S2 in Supporting Information; Casale, 2011). The fisheries of Cyprus, Egypt and Libya are each responsible for at least 2700 deaths each, predominantly in set nets, with the exception of Libya where most deaths occur in pelagic longlines and bottom trawls (Casale, 2011; see Table S1 in Supporting Information, see Fig. S2).

The mortalities described in the current study occurred in shallow (Table 1), near-shore waters in populated areas with small-scale/semi-industrial fishing fleets (Latakia Harbour, Syria: Rees *et al.*, 2010b; Lake Bardawil, Egypt: Nada *et al.*, 2013; Kyrenia Harbour, North Cyprus: Snape *et al.*, 2013). Such shallow waters are not likely to be used by larger vessels using more industrial methods such as bottom trawls, and in all of these countries, the greatest proportion of fisheries deaths occur in set nets (see Fig. S2).

Although the method that we employed to estimate mortality in the current study has been subject to some debate (Chaloupka *et al.*, 2004; Hays *et al.*, 2004; Bradshaw, 2005), the estimate should be treated conservatively, as the observed death of Turtle AA was not detectable from telemetry and so further deaths may have gone unreported. The survival probability for adults of this rookery may therefore be of a similar magnitude to estimates from other adult loggerhead populations subject to high fishing pressures of 0.81 (Frazer, 1983) and 0.88 (Chaloupka & Limpus, 2002).

Prioritizing research

Bycatch mitigation measures are more likely to be supported in small-scale fisheries if their impact on fisher livelihoods is minimized. Meanwhile, such measures should provide protection for large numbers of the most valuable demographic groups, to adequately reduce the impact of tolls. Appropriate spatial and temporal limits to any mitigation measure must be set according to detailed information on bycatch rates by specific fishery métiers. The available information both on Mediterranean loggerhead turtle habitat use and on fisheries characteristics is, however, currently insufficient, and a three pronged approach is required to address this.

Firstly, loggerhead turtle tracking studies from sites in eastern Greece, Turkey, Libya and the Levant are required to fill remaining gaps in the literature on post-nesting behaviour of the Mediterranean population. It is important that satellite telemetry studies in these rookeries, as well as in Cyprus, should aim to include male turtles. In a warming world where male numbers may decline because of the temperature-dependant sex determination of marine turtle offspring, an understanding of male movements and mortality rates is critical (Hays *et al.*, 2014). Secondly, the value of tracking studies could be amplified using predictive habitat models that incorporate remotely sensed environmental data (Jonsen *et al.*, 2007; Pikesley *et al.*, 2013; Hacothen-Domené *et al.*, 2015). In addition, localized empirical studies using aerial surveys (Cardona *et al.*, 2005), monitoring coastlines for stranded turtles (Scherer *et al.*, 2014) and surveys in fisheries (Carman *et al.*, 2011) could further delimit important foraging habitats and their demographics. Thirdly, more detailed small-scale fisheries characterization studies are required to break down marine turtle bycatch not only by gear type, but also with descriptions of individual deployment characteristics, summarizing temporal and spatial variability in

deployments of specific gear–target catch combinations. Such studies have been undertaken in Cyprus (Snape *et al.*, 2013) and are urgently needed for trawls and set nets in Tunisia, trawls and demersal longlines in Libya and set nets in Egypt, where annual mortalities of marine turtles are thought to be of many thousands (see Table S1, see Fig. S2; Casale, 2011).

However, many of the countries which host loggerhead turtle foraging grounds described here are currently facing political and economic instability which will hinder local research and conservation efforts for the near future. Despite this, by remotely assessing broad habitat use, tracking studies such as ours are a critical first step towards directing such efforts.

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REFERENCES

- Bolten, A.B. (1999) Techniques for Measuring Sea Turtles. *Research and management techniques for the conservation of sea turtles* (ed. by K.L. Eckert, K.A. Bjorndal, F.A. Abreu-Grobois and M. Donnelly), pp. 110–114. IUCN/SSC Marine Turtle Specialist Group, Washington DC.
- Bowen, B.W., Abreu-Grobois, F.A., Balazs, G.H., Kamezaki, N., Limpus, C.J. & Ferl, R.J. (1995) Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 3731–3734.
- Bradshaw, C.J.A. (2005) Survival of the fittest technology – Problems estimating marine turtle mortality. *Marine Ecology Progress Series*, **287**, 261–262.
- Broderick, A.C. & Godley, B.J. (1996) Population and nesting ecology of the Green Turtle, *Chelonia mydas*, and the Loggerhead Turtle, *Caretta caretta*, in northern Cyprus. *Zoology in the Middle East*, **13**, 27–46.
- Broderick, A.C., Glen, F., Godley, B.J. & Hays, G.C. (2002) Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx*, **36**, 227–235.

- Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F. & Godley, B.J. (2007) Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **274**, 1533–1538.
- Cardona, L., Revelles, M., Carreras, C., San, Félix M., Gazo, M. & Aguilar, A. (2005) Western Mediterranean immature loggerhead turtles: Habitat use in spring and summer assessed through satellite tracking and aerial surveys. *Marine Biology*, **147**, 583–591.
- Carman, V.G., Álvarez, K.C., Prosdocimi, L., Inchaurreaga, M.C., Dellacasa, R.F., Faiella, A., Echenique, C., González, R., Andrejuk, J., Mianzan, H.W., Campagna, C. & Albarreda, D.A. (2011) Argentinian coastal waters: A temperate habitat for three species of threatened sea turtles. *Marine Biology Research*, **7**, 500–508.
- Carreras, C., Pascual, M., Cardona, L., Aguilar, A., Margaritoulis, D., Rees, A., Türkozan, O., Levy, Y., Gasith, A., Auraggi, M. & Khalil, M. (2006) The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. *Conservation Genetics*, **8**, 761–775.
- Carreras, C., Pascual, M., Cardona, L., Marco, A., Bellido, J.J., Castillo, J.J., Tomás, J., Raga, J.A., Sanfélix, M., Fernández, G. & Aguilar, A. (2011) Living together but remaining apart: Atlantic and Mediterranean loggerhead sea turtles (*Caretta caretta*) in shared feeding grounds. *The Journal of Heredity*, **102**, 666–677.
- Casale, P. & Margaritoulis, D. (2010) Overview. *Sea turtles in the Mediterranean: distribution, threats and conservation priorities* (ed. by P. Casale and D. Margaritoulis), pp. 1–294. IUCN, Gland.
- Casale, P. (2011) Sea turtle by-catch in the Mediterranean. *Fish and Fisheries*, **12**, 299–316.
- 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. *Marine Biology*, **160**, 703–718.
- Casale, P. (2015) *Caretta caretta* (Mediterranean subpopulation). The IUCN Red List of Threatened Species. Version 2015. Available at www.iucnredlist.org (accessed 10 January 2016).
- Chaloupka, M.Y. & Limpus, C.J. (2002) Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Marine Biology*, **140**, 267–277.
- Chaloupka, M., Parker, D. & Balazs, G. (2004) Tracking turtles to their death - reply to Hays et al. *Marine Ecology Progress Series*, **283**, 301–302.
- Clarke, S.C., Harley, S.J., Hoyle, S.D. & Rice, J.S. (2013) Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. *Conservation Biology*, **27**, 197–209.
- Coyne, M.S. & Godley, B.J. (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Marine Ecology Progress Series*, **301**, 1–7.
- Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005) Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science*, **307**, 249–250.
- Frazer, N.B. (1983) Survivorship of adult female loggerhead sea turtles, *Caretta caretta*, nesting on Little Cumberland Island, Georgia, USA. *Herpetologica*, **39**, 436–447.
- Garofalo, L., A. Mastrogiacomo, P. Casale, R. Carlinie, C. Elenif, D. Freggi, D. Gelli, L. Knittweis, Mingozi Mifsud, and T., Novarini, L., Scaravelli, D., Scillitani, G., Oliverioc, M & Novelletto, A. . 2013. “Genetic characterization of central Mediterranean stocks of the loggerhead turtle (*Caretta caretta*) using mitochondrial and nuclear markers, and conservation implications.” *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 868–884.
- Godley, B.J., Richardson, S., Broderick, A.C., Coyne, M.S., Glen, F. & Hays, G.C. (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography*, **25**, 352–362.
- Godley, B.J., Broderick, A.C., Glen, F. & Hays, G.C. (2003) Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking. *Journal of Experimental Marine Biology and Ecology*, **287**, 119–134.
- Godley, B.J., Blumenthal, J.M., Broderick, A.C., Coyne, M., Godfrey, M., Hawkes, L. & Witt, M. (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research*, **4**, 3–22.
- Griffin, D.B., Murphy, S.R., Frick, M.G., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M.G., 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. *Marine Biology*, **160**, 3071–3086.
- Hacohen-Domené, A., Martínez-Rincón, R.O., Galván-Magaña, F., Cárdenas-Palomo, N., de la Parra-Venegas, R., Galván-Pastoriza, B. & Dove, A.D.M. (2015) Habitat suitability and environmental factors affecting whale shark (*Rhincodon typus*) aggregations in the Mexican Caribbean. *Environmental Biology of Fishes*, **98**, 1953–1964.
- Hammond, P.S., Macleod, K., Berggren, P. et al. (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation*, **164**, 107–122.
- 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 loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Marine Ecology Progress Series*, **233**, 273–281.
- Hawkes, L.A., Broderick, A.C., Coyne, M.S., Godfrey, M.H., Lopez-Jurado, L.F., Lopez-Suarez, P., Merino, S.E., Varo-Cruz, N. & Godley, B.J. (2006) Phenotypically linked

- dichotomy in sea turtle foraging requires multiple conservation approaches. *Current Biology*, **16**, 990–995.
- Hawkes, L.A., Witt, M.J., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M., 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. *Diversity and Distributions*, **17**, 624–640.
- Hays, G.C., Webb, P.I., Hayes, J.P., Priede, I.G. & French, J. (1991) Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. *Journal of the Marine Biological Association of the UK*, **71**, 743–746.
- Hays, G.C., Broderick, A.C., Godley, B.J., Luschi, P. & Nichols, W.J. (2003) Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. *Marine Ecology Progress Series*, **262**, 305–309.
- Hays, G.C., Broderick, A.C., Godley, B.J., Luschi, P., Nichols, W.J., Chaloupka, M., Parker, D. & Balazs, G. (2004) Tracking turtles to their death. *Marine Ecology Progress Series*, **283**, 299–302.
- 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**, 1–9.
- Hodgson, A., Kelly, N. & Peel, D. (2013) Unmanned Aerial Vehicles (UAVs) for Surveying Marine Fauna: A Dugong Case Study. *PLoS One*, **8**, e79556.
- James, M.C., Davenport, J. & Hays, G.C. (2006) Expanded thermal niche for a diving vertebrate: A leatherback turtle diving into near-freezing water. *Journal of Experimental Marine Biology and Ecology*, **335**, 221–226.
- Jonsen, I.D., Myers, R.A. & James, M.C. (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, **337**, 255–264.
- Laurent, L., Casale, P., Bradai, M.N., Godley, B.J., Gerosa, G., Broderick, A.C., Schroth, W., Schierwater, B., Levy, A.M., Freggi, D., Abd El-Mawla, E.M., Hadoud, D.A., Gomati, H.E., Domingo, M., Hadjichristophorou, M., Kornaraky, L., Demirayak, F. & Gautier, C. (1998) Molecular resolution of marine turtle stock composition in fishery bycatch: a case study in the Mediterranean. *Molecular Ecology*, **7**, 1529–1542.
- Lauriano, G., Panigada, S., Casale, P., Pierantonio, N. & Donovan, G. (2011) Aerial survey abundance estimates of the loggerhead sea turtle *Caretta caretta* in the Pelagos Sanctuary, northwestern Mediterranean Sea. *Marine Ecology Progress Series*, **437**, 291–302.
- Lewis, R., Crowder, L., Read, A. & Freeman, S. (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution*, **19**, 598–604.
- Luschi, P. & Casale, P. (2014) Movement patterns of marine turtles in the Mediterranean Sea: a review. *Italian Journal of Zoology*, **81**, 1–18.
- Margaritoulis, D. (1988) Post-nesting movements of loggerhead Sea Turtles tagged in Greece. *Rapports et Procès-verbaux des réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, **31**, 283–284.
- Margaritoulis, D. & Rees, A.F. (2011) Loggerhead turtles nesting at Rethymno, Greece, prefer the Aegean Sea as their main foraging area. *Marine Turtle Newsletter*, **131**, 12–14.
- Maxwell, S.M., Hazen, E.L., Bograd, S.J. *et al.* (2013) Cumulative human impacts on marine predators. *Nature Communications*, **4**, 2688.
- Nada, M.A., Boura, L., Grimanis, K., Schofield, G., El-Alwany, M.A., Noor, N., Ommeran, M.M. & Rabia, B. (2013) Egypt's Bardawil Lake: Safe haven or deadly trap for sea turtles in the Mediterranean? A report by MEDASSET, Suez Canal University and Nature Conservation Egypt. pp. 79.
- Palczyn, M., Hammill, E., Karpouzi, V. & Pauly, D. (2015) Population Trend of the World's Monitored Seabirds, 1950–2010. *PLoS One*, **10**, e0129342.
- Pfaller, J.B., Bjorndal, K.A., Chaloupka, M., Williams, K.L., Frick, M.G. & Bolten, A.B. (2013) Accounting for Imperfect Detection is Critical for Inferring Marine Turtle Nesting Population Trends. *PLoS One*, **8**, e62326.
- Pikesley, S.K., Maxwell, S.M., Pendoley, K., Costa, D.P., Coyne, M.S., Formia, A., Godley, B.J., Klein, W., Makanga-Bahouna, J., Maruca, S., Nguouesso, S., Parnell, R.J., Pemo-Makaya, E. & Witt, M.J. (2013) On the front line: integrated habitat mapping for olive ridley sea turtles in the southeast Atlantic. *Diversity and Distributions*, **19**, 1518–1530.
- Rees, A.F., Al Saady, S., Broderick, A.C., Coyne, M.S., Papatathanasopoulou, N. & Godley, B.J. (2010a) Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*. *Marine Ecology Progress Series*, **418**, 201–212.
- Rees, A.F., Saad, A. & Jony, M. (2010b) Syria. *Sea turtles in the Mediterranean: distribution, threats and conservation priorities* (ed. by P. Casale and D. Margaritoulis), pp. 233–243. IUCN, Gland.
- Revelles, M., Carreras, C., Cardona, L., Marco, A., Bentivegna, F., Castillo, J.J., de Martino, G., Mons, J.L., Smith, M.B., Rico, C., Pascual, M. & Aguilar, A. (2007) Evidence for an asymmetrical size exchange of loggerhead sea turtles between the Mediterranean and the Atlantic through the Straits of Gibraltar. *Journal of Experimental Marine Biology and Ecology*, **349**, 261–271.
- Robinson, R.A., Crick, H.Q.P., Learmonth, J.A. *et al.* (2009) Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, **7**, 87–99.
- Rodhouse, P., Prince, P., Trathan, P., Hatfield, E., Watkins, J., Bone, D., Murphy, E. & White, M. (1996) Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. *Marine Ecology Progress Series*, **136**, 37–50.
- Scherer, A.L., Valls, F.C.L., Basler, A.B., Scherer, J.D.M. & Petry, M.V. (2014) Life Stages, Anthropogenic Impact, and Temporal Variation of Stranded Sea Turtles in Southern Brazil. *Chelonian Conservation and Biology*, **13**, 42–48.

- Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A. & Hays, G.C. (2010) Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions*, **16**, 840–853.
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, A., Koutsoubas, D., Lilley, M.K.S., Pantis, J.D., Karagouni, A.D. & Hays, G.C. (2013) Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Diversity and Distributions*, **19**, 834–844.
- Snape, R.T.E., Beton, D., Broderick, A.C., Çiçek, B.A., Fuller, W.J., Özden, Ö. & Godley, B.J. (2013) Strand monitoring and anthropological surveys provide insight into marine turtle bycatch in small-scale fisheries of the eastern Mediterranean. *Chelonian Conservation and Biology*, **12**, 44–55.
- Snoddy, J. & Southwood Williard, A. (2010) Movements and post-release mortality of juvenile sea turtles released from gillnets in the lower Cape Fear River, North Carolina, USA. *Endangered Species Research*, **12**, 235–247.
- Spotila, J.R., Reina, R.D., Steyermark, C., Plotkin, P.T. & Paladino, F.V. (2000) Pacific leatherback turtles face extinction. *Nature*, **405**, 529–530.
- Stokes, K.L., Broderick, A.C., Canbolat, A.F., Candan, O., Fuller, W.J., Glen, F., Levy, Y., Rees, A.F., Rilov, G., Snape, R.T.E., Stott, I., Tchernov, D. & Godley, B.J. (2015) Migratory corridors and foraging hotspots: critical habitats identified for Mediterranean green turtles. *Diversity and Distributions*, **21**, 665–674.
- Tucker, A.D. (2010) Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: Implications for stock estimation. *Journal of Experimental Marine Biology and Ecology*, **383**, 48–55.
- Wallace, B.P., Heppell, S.S., Lewison, R.L., Kelez, S. & Crowder, L.B. (2008) Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses. *Journal of Applied Ecology*, **45**, 1076–1085.
- Wallace, B.P., Lewison, R.L., McDonald, S.L., McDonald, R.K., Kot, C.Y., Kelez, S., Bjorkland, R.K., Finkbeiner, E.M., Helmbrecht, S. & Crowder, L.B. (2010) Global patterns of marine turtle bycatch. *Conservation Letters*, **3**, 131–142.
- Wallace, B.P., DiMatteo, A.D., Bolten, A.B. *et al.* (2011) Global conservation priorities for marine turtles. *PLoS One*, **6**, e24510.
- Witt, M.J., Åkesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C., Luschi, P., Stroud, S. & Godley, B.J. (2010) Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Animal Behaviour*, **80**, 571–581.
- Witt, M.J., Augowet Bonguno, E., Broderick, A.C., Coyne, M.S., Formia, A., Gibudi, A., Mounquengui Mounquengui, G.A., Moussounda, C., Nsafou, M., Nougessono, S., Parnell, R.J., Sounguet, G.P., Verhage, S. & Godley, B.J. (2011) Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **278**, 2338–2347.
- Zbinden, J.A., Bearhop, S., Bradshaw, P., Gill, B., Margaritoulis, D., Newton, J. & Godley, B.J. (2011) Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Marine Ecology Progress Series*, **421**, 291–302.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. 20% (dark grey) and 50% (light grey) data distribution isopleths produced from kernelled filtered satellite telemetry data for turtles foraging in (a) Lebanon, (b) East Libya (c) Central Libya and (d) Central-West Libya.

Figure S2. Stacked bar plot of estimated annual marine turtle mortalities by gear types (PL = Pelagic Longline, DL = Demersal Longline, SN = Set Net, BT = Bottom Trawl) for the main countries that host foraging loggerhead turtles tracked after nesting in North Cyprus (Cyp = Cyprus, Syr = Syria, Egy = Egypt, Lib = Libya, Tun = Tunisia). Calculated according to numbers of turtle captures per year and gear type-specific mortality rates compiled and estimated by Casale (2011) and Snape *et al.* (2013).

Table S1. Captures, mortality rate estimates and deaths of marine turtles caught in main fisheries of Cyprus, Syria, Egypt, Libya and Tunisia. Sources: 1 = Casale (2011); 2 = Snape *et al.* (2013).

BIOSKETCH

Robin Snape is an ecologist at the Marine Turtle Research Group (www.seaturtle.org/MTRG). Robin lives and works in North Cyprus where he has a managerial role in long-term monitoring and conservation of marine turtles through the Marine Turtle Conservation Project and North Cyprus Society for Protection of Turtles (www.cyprusturtles.org). This work constitutes part of his PhD with BJB and ACB at the University of Exeter.

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