

Spatiotemporal hotspots of habitat use by loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles in the Levant basin as tools for conservation

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ABSTRACT: Understanding the spatiotemporal abundance of loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles is crucial for marine conservation. In Israel, at the south-eastern Levant Sea, 10 loggerhead (8 females, 2 males) and 5 green (3 females, 2 males) sea turtles were tracked via satellite telemetry tags. Turtles were tagged post nesting ($n = 8$) or prior to their release following rehabilitation ($n = 7$, 3 females and 4 males, all sub-adults to adults). Tracked sea turtles spent their time foraging in a median of 137 km² core home range (50% kernel density estimation). Home range size increased to a median of 464 km² during the inter-nesting season. Migration varied widely, ranging from 87 km from the tagging site in 1 turtle (near residency) to >3000 km in 2 other turtles. Most turtles migrated short distances within the south-eastern Levant Sea, which seems to be a multifunctional habitat for reproduction, migration and foraging. A large proportion of the migrations (72%) occurred along the coastline and the rest were in open waters. These new insights regarding the spatial distribution of sea turtles over the course of the year may potentially be translated into conservation guidelines, such as seasonal fishing restrictions, and management and planning of marine protected areas in the south-eastern Mediterranean Sea.

KEY WORDS: Home range · Migration corridors · Feeding grounds · Green sea turtle · Loggerhead sea turtle · Seasonal patterns · Conservation · Marine protected area · MPA

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INTRODUCTION

The vast exploitation of the sea by the commercial fishing (Wallace et al. 2010) and energy industries (including seismic surveys for oil and gas exploration; Nelms et al. 2016), coastal development (Casale & Margaritoulis 2010), maritime trade transportation, communication infrastructures and pollution (Bjorndal & Jackson 2003) threaten marine ecosystems worldwide, increasing the need for conservation regulations (Broderick et al. 2007, Schofield et al. 2010b, Wallace et al. 2010, Stokes et al. 2015). Intense historical harvesting has left most sea turtle populations severely depleted (Seminoff & Shanker 2008), and while some

have shown an encouraging rebound capacity (Chaloupka et al. 2008), incidental bycatch has impeded recovery in other areas (Hays et al. 2003, Lewison et al. 2004, Stokes et al. 2015).

In the Mediterranean, sea turtles were targeted historically by the fishing industry, with an annual average of 2000 turtles caught during the 1930s in the south-eastern basin alone (Hornell 1935). As a result, the local populations of both loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles declined severely. Today, the intentional capture of marine turtles is illegal, but turtles are still frequently caught by the fishing industry as bycatch, leading to extremely high mortality rates (Levy et al.

2015). The Mediterranean Sea is considered to have the highest fishery bycatch rates in the world (Wallace et al. 2010, 2011, Casale 2011), and the south-eastern Mediterranean Sea (also known as the Levant basin) has the highest sea turtle mortality rate in the Mediterranean (more than 1 stranded turtle per km; Levy et al. 2015), leaving the regional turtle population at a high risk of extinction.

In the Mediterranean Sea, loggerheads breed mainly in the eastern basin, while green turtles restrict their reproduction area to the Levant basin alone (Casale 2011, Levy et al. 2015). The nesting season occurs from mid-May to the beginning of August, peaking between June and the middle of July (Levy 2005, Levy et al. 2015), simultaneously with the neighboring Mediterranean nesting sites (Casale & Margaritoulis 2010, Schofield et al. 2013b). A study conducted in Zakynthos, Greece, revealed a variation in home range sizes during nesting season: male loggerheads shared a stable core 5 km (50% kernel estimator) nearshore range, and the broadest nesting home range (95%) had a mean of 21 km². Female home ranges were approximately twice those sizes (Schofield et al. 2010b). Outside the Mediterranean Sea, larger inter-nesting home ranges (mean 559 km²) have been documented in loggerhead sea turtles in Brazil (Marcovaldi et al. 2010). The breeding home range of green sea turtles is poorly documented in the literature but has been studied in the Florida Keys, where the turtles spent large periods of their time within the 160 km² study site (Hart et al. 2013). Large home ranges have been described in other species as well: the breeding home range of Kemp's ridley turtles in Texas (Shaver et al. 2005, Seney & Landry 2008) is reported to be up to 1000 km², and up to 6000 km² of habitat is utilized by breeding Atlantic leatherbacks (James et al. 2005, Eckert et al. 2006, Schofield et al. 2010b). At the end of the breeding season in the Mediterranean, turtles mainly migrate along the coast but also in the open sea through specific migration corridors to their foraging grounds in the central and eastern Mediterranean Sea (Hays et al. 2014a, Stokes et al. 2015, Snape et al. 2016). The foraging home range sizes documented in studies from Greece (Schofield et al. 2010b) and north Cyprus (Snape et al. 2016) appear to range from 10s to 100s of km². All tagged turtles from north Cyprus were found in areas with between 2 and 121 m bottom depth in 5 major foraging grounds, which is suggestive of benthic feeding. A common pattern observed in several loggerhead studies is that foraging areas are generally larger for turtles residing offshore and in deeper water than for those close to the coast (Schofield et al. 2010a).

Several studies conducted in Zakynthos, Greece, revealed a variation in foraging home range size, ranging from circa 10 km² at neritic habitats to ~1000 km² at oceanic sites (Schofield et al. 2010a). A different study revealed a mean foraging home range of 305 km² (Zbinden et al. 2008), and in Cyprus, a difference was found in home range size between winter and summer in both loggerhead (55 and 331 km², respectively) and green turtles (37 and 77 km², respectively) (Broderick et al. 2007). Outside the Mediterranean Sea, foraging home ranges were found to range from 545 to 1501 km² and from 570 to 2700 km² in different studies in Brazil (Marcovaldi et al. 2010). A smaller foraging home range (mean 237 km²) was found in Cape Verde (Hawkes et al. 2006) and a mean of 52 km² in the Northwestern Atlantic USA (Hawkes et al. 2007). Green sea turtles forage in oceanic and neritic sites (Seminoff et al. 2008) and are expected to use a smaller foraging home range than loggerhead sea turtles (Broderick et al. 2007). Still, home range size varies widely, from a range of 2 to 9 km² in San Diego, CA, USA (MacDonald et al. 2012) to approximately 4 to 40 km² in Mexico (Seminoff et al. 2002).

It is important to notice that some of these differences may well be attributed to differences in accuracy between different tags. While GPS loggers and Fastloc tags are accurate to 10s of meters (Schofield et al. 2010b), the conventional Argos transmitters are less accurate (maximum accuracy is ~150 m) (Schofield et al. 2009). The advantage of satellite telemetry can be great if recapture reliance is low due to political borders and low turtle encounters. Satellite telemetry has been used to identify areas of high use, predict spatial distribution of marine turtle bycatch and evaluate the potential effectiveness of conservation measures (Makowski et al. 2006, Hawkes et al. 2011, Schofield et al. 2013a, Stokes et al. 2015).

Not discounting the immense value of the data already acquired by worldwide studies, regional conservation programs must be based on locally relevant information regarding sea turtle spatiotemporal distribution. As topographical characteristics and environmental conditions vary over different geographical areas, local research is required to identify major turtle activity sites such as important feeding grounds, migration corridors, seasonal dynamics and home ranges (Katselidis et al. 2013, Mazaris et al. 2014, Pendoley et al. 2014, Almpandou et al. 2016, Shaver et al. 2016).

In the Mediterranean Levant basin, sea turtles were documented in their thousands during the 1930s (Gruvel 1931, Hornell 1935), feeding and mating or just migrating. In 2010, only around 100 nests

of loggerhead and green turtles were reported annually from each of the countries Syria, Lebanon, Israel and Egypt (Casale & Margaritoulis 2010).

Nowadays, in Israel, the number of nests has doubled (Israel Nature and Parks Authority unpubl. data). The Israel Sea Turtle Rescue Center treats 50 to 80 injured sea turtles every year (unpubl. data), most of them suffering from fishing related injuries, and also documents more than 200 sightings of stranded sea turtles annually (Levy et al. 2015). Carapace length distribution of sea turtles, documented by the Israel Nature and Parks Authority, reveals that this area serves both young and adult turtles (unpubl. data). Efforts to protect the local and transient population include the declaration of several marine reserves (some are still under the legislative process), a long-term nest relocation program, and a rescue center that treats wounded turtles and holds green turtles for breeding to increase the number of hatchlings released. The center also conducts research and works to increase public awareness through tours, volunteering opportunities and media engagement.

In this study, we used satellite transmitters to track 15 adult sea turtles (both loggerheads and green sea turtles) in order to determine priority habitats for marine turtle protection along the Israeli coast and beyond—a region where turtles are known to be heavily impacted by fisheries (Snape et al. 2016).

MATERIALS AND METHODS

A total of 15 sea turtles were tracked between 2008 and 2015 using PTTs (Platform Terminal Transmitters; Sirtrack: KiwiSat101, $n = 10$, Wildlife Computers: SPOT5, $n = 5$). The tagged turtles included 8 nesting females (5 loggerhead *Caretta caretta* and 3 green *Chelonia mydas*), and 7 rehabilitated turtles (2 male and 3 female loggerhead and 2 male green turtles, all treated at the Israel Sea Turtle Rescue Center for fishery-related injuries, see Table 1). All tagged turtles were adults, with curved carapace length ranging from 66.5 to 78.5 cm in the loggerhead sea turtles, and 68.4 to 86.5 cm in the green sea turtles. Transmitters were attached using epoxy resin following the methodology of Godley et al. (2002). Track locations were obtained via the Argos satellite tracking system, and were downloaded, stored and managed using the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005). Maximum Argos data accuracy was circa 150 m. Tracks were processed and mapped using R (R Core Team 2015), ArcGIS 10.3 software with the Spatial Analyst extension, Geospatial Model-

ling Environment (GME) and QGIS 2.8.9. A Best Daily Location (BDL) filter was applied to the already filtered datasets (in which dry locations, location class Z and less than 2 messages in B were excluded). The BDL filter graded transmissions by their class rank and number of messages, and chose the location with the median bottom depth in the case of ties.

Activity characterization

Tracks were divided into nesting, migrating and foraging phases, using displacement plots and visual assessment (Blumenthal et al. 2006, Stokes et al. 2015). The nesting phase refers to the activities of female turtles during the nesting season. The migration phase consisted of post-nesting and post-release tracks. The foraging phase consisted of transmissions that continued from the end of migration for at least 38 d to indicate conclusive residency.

Temporal activity patterns

In order to describe seasonal patterns in turtle activity, we analysed the annual distribution of turtles during nesting, migrating and foraging by calculating the frequencies of turtles performing each of the 3 activities. To better identify seasonal effects, we excluded the year factor and regarded only day of the year.

Spatial distribution

The spatial distribution of migrating, nesting and foraging turtles was analysed from 2 perspectives: geographical location of the habitat (or migration route) and its characteristics, distance from shore, bottom depth and home range size—all of significant value to conservation efforts. To visualize turtle geographic locations and identify active hotspots and migration corridors, we created a raster of the number of all tagged turtle tracks crossing each cell of a hexagonal grid (0.125° by 0.125° each) covering the study area. Hexagons with only 1 transmission were excluded (except for hexagons overlapping land).

Home range

Home range estimation was done for each of the tagged turtles, and then separately for the nesting

and foraging phases. This analysis was only performed for turtles for which 13 or more locations (d) were recorded independently in each phase. As migration is the transition between home ranges and usually follows a directional path, no home range was estimated for migrating turtles. We used Kernel density estimation to quantify the size of the area in which each turtle performed either foraging or nesting behavior, and visualized the results by projecting the 95 and 50% contours on a map. Several algorithms for determining the bandwidth factor (e.g. least-squares cross-validation were examined in GME software (Stokes et al. 2015), and when examined visually, were found to be influenced by the spatial orientation of the observations (Gredzens et al. 2014). In addition, in cases of observations near the coast, the density estimation output reached far inland for several algorithms (e.g. likelihood cross-validation). Therefore, we choose to use a fixed bandwidth factor (Shillinger et al. 2008, Witt et al. 2010) of 0.1 decimal degrees for all data sets. Cell size was fixed to 0.005 decimal degrees. In GME, kernel continuous outputs were converted to polygons that delimited a defined percent of the density surface, representing 50, 75 and 95% of the original observation home range. Median home range for actively nesting or foraging turtles was estimated using a bootstrap method, and differences in medians were tested using a randomized *t*-test (see 'Statistical analysis'). We defined foraging grounds as the core home range of foraging turtles, estimated as the 50% kernel density contour (Schofield et al. 2010b, Snape et al. 2016).

To characterize habitats preferred by sea turtles, 2 more spatial parameters were estimated for all 3 activities (nesting, migrating and foraging): bottom depth and distance from shore at the turtle locations.

Bottom depth

Bottom depth for each best daily location (per turtle) was sampled from bathymetry data of the General Bathymetric Chart of the Oceans GEBCO 1-Minute Global Bathymetry Grid (https://www.bodc.ac.uk/data/hosted_data_systems/gebco_gridded_bathymetry_data/gebco_one_minute_grid/) via STAT (Coyné & Godley 2005). To estimate bottom depth of the turtle location for each activity, each turtle was assigned the median value of bottom depth recorded when performing a given activity, estimated using the bootstrap method (see 'Statistical analysis'). Median bottom depth per activity was then estimated

based on the median bottom depth previously assigned to each turtle performing that activity (again using the bootstrap method). Differences in median bottom depths between the different activities were then tested using randomized 1-way ANOVA (via the 'Imperm' package in the R software, see 'Statistical analysis').

Distance from shore

The distance from shore for each best daily location was estimated using the NEAR function from the nearest shoreline (ArcGIS 10.3). The Environmental Systems Research Institute (ESRI) ArcGIS global layer was used as a baseline. In convoluted coastlines, mapping accuracy was improved by digitisation on the basis of ESRI satellite imagery. Estimation of the distribution of distances and their medians was carried out as described for bottom depths. Similarly, differences in median distance from shore between different activities were tested using randomized 1-way ANOVA (via the 'Imperm' package in the R software, see 'Statistical analysis').

Statistical analysis

Throughout the study, sample size and non-normal distributions often restricted the statistical analysis. For this reason, we adopted non-parametric and randomized methods for both parameter estimation and hypothesis testing.

As distributions of home ranges, bottom depths and distances from shore were often non-symmetrical, medians were preferred over mean values as measures of central tendency. To diminish effects of small sample size, all median values were estimated using a standard bootstrap resampling method (Efron 1979, Efron & Tibshirani 1994, Manly 2007). The essence of this technique is the idea that given no additional information about the population, resampling with replacement from the obtained sample is the best approximation to actual resampling from the population. When bootstrapping, each resampling is done with replacement so that each bootstrap sample is slightly different from the others, resulting in a different parameter value. Given a high enough number of resamples (1000 to 10 000), the parameter distribution is expected to sufficiently represent that distribution in the general population from which the sample was initially obtained. Thus, the mean or median value of the parameter distribution is a good estimate

for that parameter in the population. Furthermore, given the parameter distribution estimated by bootstrap resampling, additional measures of accuracy can be estimated including standard error and confidence interval. Using this technique, we estimated median values for home range size, bottom depth and distance from shore for each turtle performing a specific activity. To account for differences in sample sizes of different turtles (as some turtles transmitted for a longer period than others), resampling was done based on a probability function, representing the number of transmissions obtained for each turtle. By doing so, a value that was estimated based on many transmissions had a higher chance of being sampled than a value that was estimated based on fewer transmissions. Bootstrapping relied on 10 000 repeats of the resampling process, to compensate for very small samples.

To test hypotheses regarding differences in the bootstrap-estimated median home range size between turtles actively nesting or foraging, we used a randomized *t*-test (R Core Team 2015). This test compares the observed difference in sample medians to a distribution of medians, inferred from the observed data itself. Since no theoretical distribution is used, there is no need to assume the population is normally distributed. In each step of the randomized *t*-test, values of home range medians were randomly divided into 2 groups ('mock' samples), with the same sample size as the 'original' samples. Medians for each mock sample were estimated using a standard bootstrap resampling method, as described above, and the difference between the medians was calculated and recorded. This process was repeated 1000 times, resulting in a distribution of the difference in medians. A *p*-value for the difference in medians was then calculated with respect to this inferred distribution, rather than a theoretical one.

Differences in bottom depth or distance from shore medians were similarly tested, using a randomized 1-way ANOVA for a 3-leveled factor (nesting, migrating and foraging). In the randomized ANOVA, the 3 samples are randomly shuffled and the variance within and between samples is recorded. Similarly to the randomized *t*-test, multiple repetitions of this shuffling process produce within and between variance distributions, to which the observed variance is compared. Further, Tukey's HSD tests were conducted to identify statistically significant differences in median bottom depths or distances from shore between nesting, migrating and foraging turtles.

RESULTS

A total of 15 sea turtles were tracked throughout the study, including 8 females tagged during the nesting season. Of the 15 turtles, 13 were documented foraging and 11 were documented migrating. The median period of tag transmissions was 217 d (range: 5 to 792 d, Table 1).

The 5 nesting loggerhead females migrated to foraging sites, where they were recorded for 28 to 206 d. Of the 3 green females that nested and migrated, 2 were recorded for 45 and 214 d at foraging sites. Two male loggerhead turtles were released, following rehabilitation, at the end of April and August (around the breeding season). None of them migrated to or away from the breeding sites, but rather remained foraging in close proximity to the release site. We obtained sufficient foraging information on 49 of 50 d and 266 of 793 d of foraging for each of the turtles. The 2 male green turtles that were released, following rehabilitation, in mid-June started migrating upon release. We obtained sufficient foraging information for 1 male on 37 of 38 d, whereas the other male stopped transmitting while migrating. The 3 rehabilitated female loggerhead turtles were released in February, August and October (according to their health state). One migrated upon release in February to the foraging site (54 d of transmissions) and 2 remained foraging around the capture and release site. We obtained sufficient foraging information on 79 of 217 d and 226 of 275 d of foraging. No rehabilitated female green turtles were tagged. All 7 rehabilitated turtles were released close to where they were found. Four of the turtles remained in the area and foraged while 3 migrated to their foraging sites (Table 1).

Temporal activity patterns

All tagged nesting females shared the same pattern of migration to their foraging grounds when the nesting season was over, and stayed in their foraging grounds for a long period of time (median 275 d), except for 2 turtles (K and N) who migrated between nearby foraging grounds.

Tag deployment for 5 nesting females was done during one of the few crawls of the season, rendering an incomplete documentation of nesting period, as the first few weeks are inherently missing from the data. The documented nesting period ranged from 11 to 52 d (median \pm SE: 16.5 \pm 7.9) from tag deployment until post-nesting migration (another 3 migrated immediately after tag deployment) (Table 1), repre-

Table 1. Details for satellite transmitter-tagged loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. Status: status at deployment; 50%: 50% home range area; Trans.: number of transmitting days; Dist.: distance travelled; Dep.: departure date; Depl.: deployment date; End: end of transmission; R: rehabilitation; N: nesting; M: male; F: female; WC: Wildlife Computers; Sir: Sir track; na: not applicable. Dates are given as dd/mm/yy

ID	Turtle		Nesting			Migrating			Dep.	Foraging			Transmission		Satellite transmitter
	Status	Sex	50% (km ²)	Trans. (d)	Period (d)	Dist. (km)	Trans. (d)	Period (d)		50% (km ²)	Trans. (d)	Period (d)	Depl.	End	
<i>Chelonia mydas</i>															
A	R	M				290 ^a	19	23 ^a	17/06/14 ^a	231	37	38	17/06/14	16/08/14	WC SPOT5
E	R	M				210 ^a	6	6 ^a	17/06/14 ^a				17/06/14	22/06/14	WC SPOT5
B	N	F				183	7	7	27/06/09	98	45	48	28/06/09	21/08/09	Sir KiwiSat101
C	N	F	908	20	20	1254	27	27	09/07/09	137	214	308	20/06/09	09/06/10	Sir KiwiSat101
D	N	F				1167	22	22	29/07/08				29/07/08	19/08/08	Sir KiwiSat101
<i>Caretta caretta</i>															
I	R	M								291	49	50	29/08/14	18/10/14	WC SPOT5
J	R	M								184	266	793	30/04/10	01/07/12	Sir KiwiSat101
F	R	F				306 ^a	19	25 ^a	22/02/09 ^a	121	54	155	22/02/09	21/08/09	Sir KiwiSat101
M	R	F								136	79	217	22/10/14	30/05/15	WC SPOT5
N	R	F								383	226	275	29/08/14	05/06/15	WC SPOT5
G	N	F	555	21	26	282	8	8	20/07/10	113	28	389	23/06/10	20/08/11	Sir KiwiSat101
H	N	F	94	13	14	3151	70	70	19/07/09	120	95	96	05/07/09	31/12/09	Sir KiwiSat101
K	N	F				3481	80	86	19/07/08	572	97	345	19/07/08	05/11/09	Sir KiwiSat101
L	N	F	na	5	11	87	1	1	19/07/09	113	169	316	08/07/09	02/06/10	Sir KiwiSat101
O	N	F	372	27	52	149	5	5	20/07/09	105	206	565	28/05/09	15/02/11	Sir KiwiSat101

^aData was excluded from post-nesting migration calculations

senting the middle to the end of the nesting season. Since no turtle was tracked long enough to document 2 consecutive breeding seasons, there is no documentation of migration from foraging grounds to breeding sites as well as expected breeding activity at the beginning of the season. Therefore, the time of arrival to nesting areas cannot be derived from the tracking data.

Migration was observed for 8 nesting females, for which the duration of the migration phase ranged from 1 to 86 d (median \pm SE: 15 \pm 27, n = 8 individuals), starting in mid-July, corresponding with the end of nesting season, and extending to November (Table 1). Seven of the 8 (87.5%) females completed their migrations between July and September. Migration of the 3 rehabilitated female turtles from location of release to their foraging grounds was not included in this analysis, as the timing was correlated with non-biological factors (their health and release time). Post-nesting females started to forage following the completion of migration (from July to November). Most (88%) of the transmission days were recorded during the foraging phase. The duration of the foraging period ranged from 38 to 793 d (median \pm SE: 275 \pm 61.03 d, n = 13 individuals (Table 1). Gaps in transmissions were included in the specific activity period in cases where turtles reappeared in the same region, manifesting similar activity characteristics.

Spatial distribution

A total of 1924 locations were filtered and used out of all the 9221 locations reported during 4090 transmission days. Location analysis revealed that loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles inhabit the south-eastern Mediterranean Sea during both nesting and foraging phases, while some migrating turtles crossed south-west towards the coast of north Africa or traveled north towards Syria.

Track density analysis revealed that most turtles tagged along the Israeli coastline remained relatively close to their release site by the eastern beaches of the Levant basin where they were engaged in all 3 activities (Fig. 1A–C). The turtle track densities during the nesting season exhibited fidelity to the nesting area (Fig. 1B) along the beaches of Israel and around Bardawil Lake, Egypt. High track density was also recorded in this region during the foraging phase (Fig. 1C). Migration track density (for both post-rehabilitation and post-nesting turtles) revealed that while some turtles crossed deep waters on their migration routes, 7 of 11 turtles (64%) migrated along the shoreline (Fig. 1A,D). Only 4 turtles (36%) migrated a distance >300 km. The home range analysis of 13 foraging turtles revealed several relatively small foraging grounds, with a median core

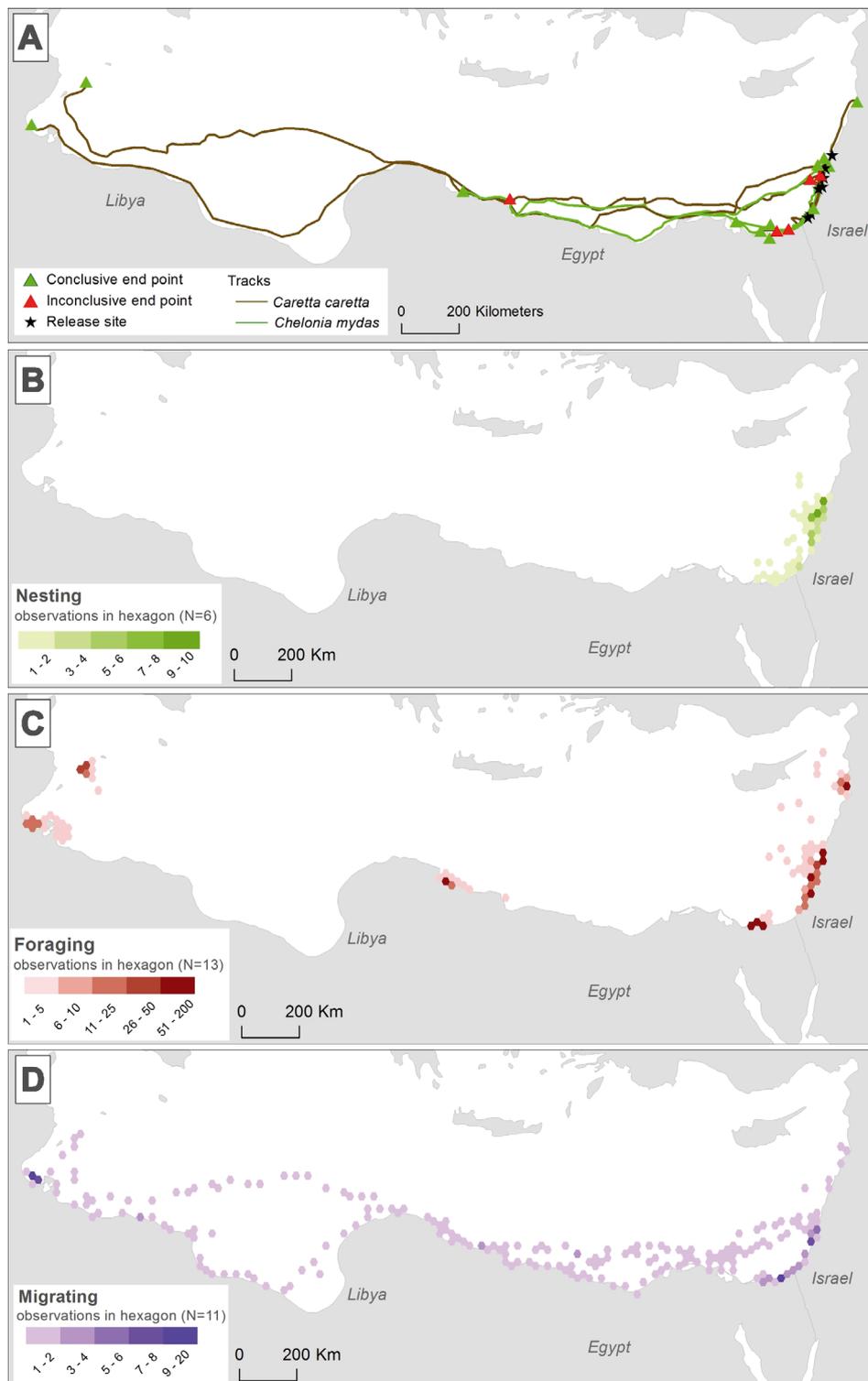


Fig. 1. (a) Spatial distribution of tagged loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles. Ten of the 15 turtles remained for a considerable period (>38 d) at the endpoint and were marked as conclusive. The 5 turtles that stopped transmitting before exhibiting residency at a certain point were marked as inconclusive endpoints. Turtle paths from tag deployment to endpoints (n = 15). (b) The number of tagged turtle tracks crossing a hexagon (1 transmission per cell was excluded, except for hexagons overlapping land), creating a grid of track density for nesting females during the nesting season (n = 6). (c) Hexagon grid of track density of actively foraging turtles (n = 13). (d) Hexagon grid of track density of migrating turtles (n = 11). Colors are indicative of the number of satellite tracks that pass through each hexagonal grid cell

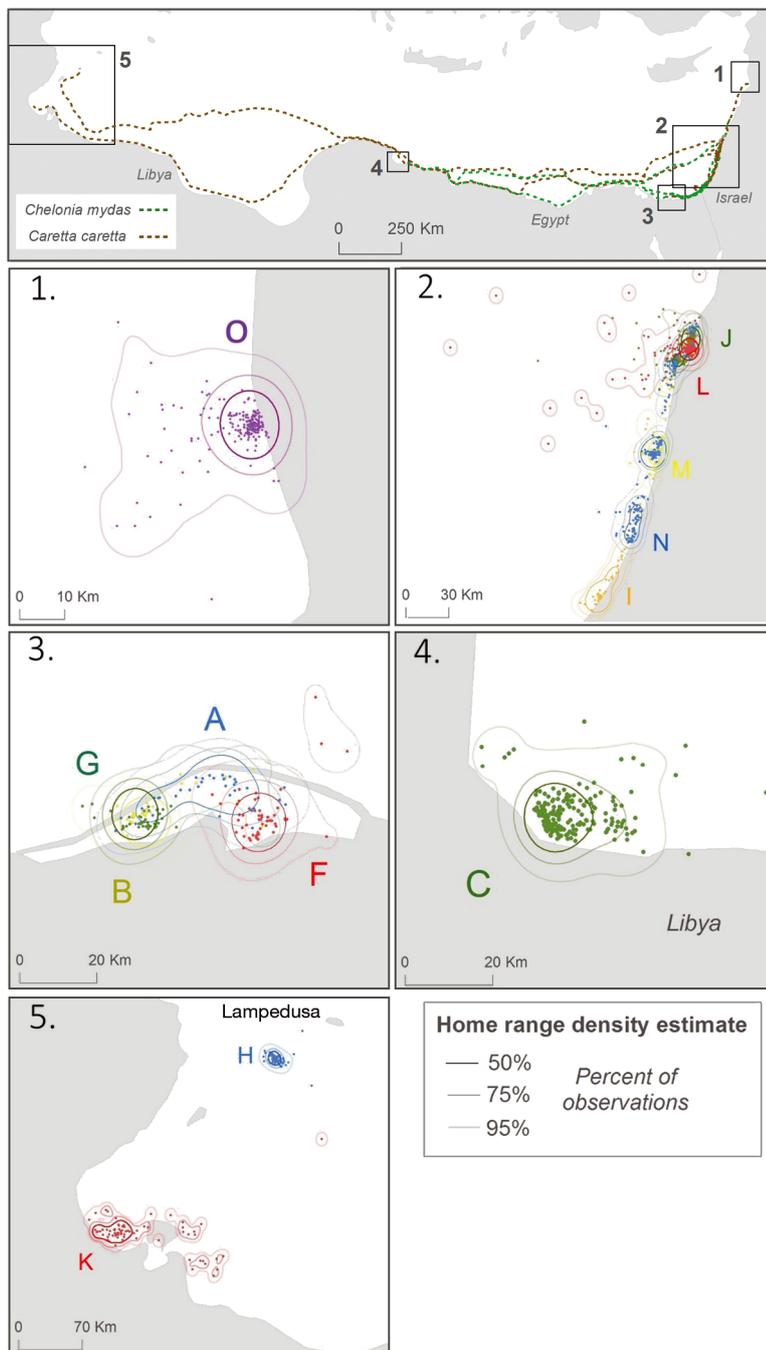


Fig. 2. Home range estimation of foraging loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles with 50, 75 and 95% kernel density contours. Foraging grounds were identified (50%, core home range) in 5 areas, numbered 1 to 5 (bold lines, 13 turtles in total indicated by the different uppercase letters): (1) Syria, (2) Israel, (3) Lake Bardawil, Egypt, (4) eastern Libya, (5) Tunisia and Lampedusa

home range (estimated as the 50% kernel density contour) of only 137 km² (SE: 32 km²). Median home range at the 95% density contour was 1092 km² (SE: 339 km²). It is likely that the estimated core home

range is larger than the actual turtle home range as the data accuracy is on a scale of 100s of meters. Foraging grounds, defined by core home ranges, were found close to shore (median \pm SE: 2.953 \pm 0.415 km from shore, CI: 2.1–4.2 km) and in relatively shallow waters (20 \pm 3 m bottom depth, CI 10–24 m). For all tested parameters, no significant or ecologically meaningful difference was found between loggerhead and green sea turtles, nor between post-nesting and post-rehabilitation turtles.

Overall, 9 foraging grounds were identified: 4 along the coast of Israel (Fig. 2, panel 2), and 5 in specific locations across Syria (panel 1), Egypt (panel 3), Libya (panel 4), Tunisia and the Italian island of Lampedusa (panel 5). Three major foraging grounds were shared by 2 or more turtles: (1) Lake Bardawil, Egypt, was the foraging site of 4 of the 13 foraging turtles (Fig. 2, panel 3); (2) the foraging ground found in Haifa Bay, Israel, was shared by 2 turtles (panel 2, marked L and J); and (3) the foraging ground found roughly 60 km south of Haifa was shared by 2 other turtles (marked M and N). The 95% density contours show marginal foraging relatively far from the coast in 2 of the 13 tracked turtles (Fig. 2, L in panel 2 and K in panel 5). Turtles K and N travelled between 2 distinct foraging grounds (N in panel 2, K in panel 5), less than 100 km apart, while the remaining 10 turtles did not stray far from their core home range.

During the nesting season, 5 female sea turtles remained close to their nesting sites, across Israeli beaches. These ranges differed from their foraging grounds, and the distances between nesting and feeding sites were >150 km for 4 of the 5 females; the fifth female was excluded due to a small number of observations (Fig. 3a). Home ranges estimated by the 95% density contour for the 4 nesting females (median \pm SE: 2138 \pm 533 km²) were twice the size of those estimated for

foraging behavior. Core home ranges of these nesting turtles (464 \pm 174 km²) were more than 3 times the size of foraging core home ranges (Fig. 3b, $p = 0.011$, randomized t -test). Nesting females appeared to stray

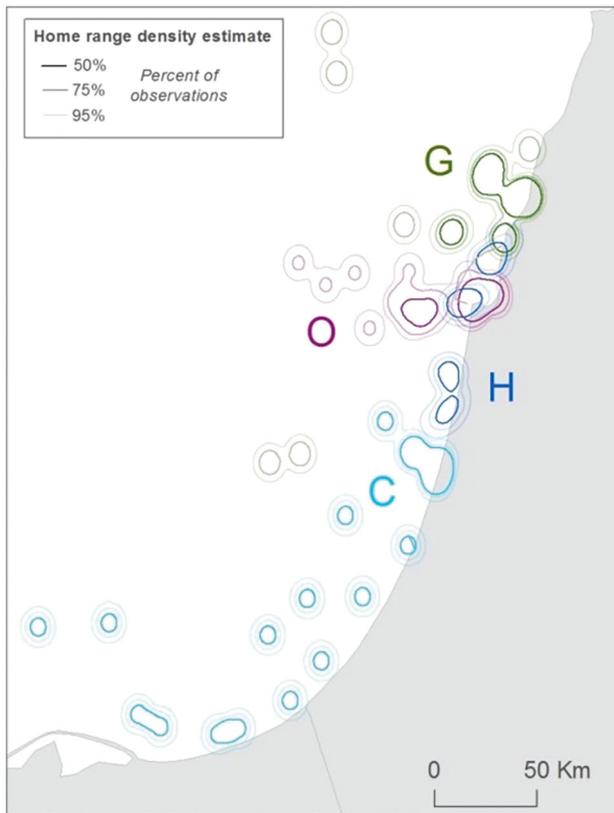


Fig. 3. Kernel density estimation for home ranges during the nesting season for 4 nesting female loggerhead (*Caretta caretta*, individuals G,H,O) and green (*Chelonia mydas*, individual C) sea turtles. (a) Density contours (50, 75 and 95 %) projected on a map of the south-eastern Mediterranean Sea

further away from the shore (12.159 ± 2.354 km from shore, $n = 5$) to deeper waters (361 ± 243 m bottom depth, $n = 5$), compared to foraging areas. However, these differences were not statistically significant. Because of the small sample size, differences in these parameters between loggerhead and green sea turtles could not be statistically tested. Nevertheless, it should be noted that the home range size of the female green sea turtle was larger than those estimated for the 3 loggerheads. However, the median bottom depth and median distance from shore of this female green sea turtle was well within the range of the medians estimated for the 4 loggerheads. No rehabilitated turtle was documented nesting. Although the inter-nesting period is shorter than the foraging period (4.4% and 88%, respectively, of all transmission days), the 50% and 75% home range densities were more than 3 times larger for nesting than for foraging (3.4 and 3.7 times larger, respectively, randomized t -test $p < 0.012$)

Post-nesting and post-rehabilitation migration distances ranged from 87 to 3481 km, with an estimated

median distance of 290 km (CI: 183–1254 km, $n = 11$ individuals). Seven of the 11 turtles (64%) migrated a relatively short distance (300 km or less). Among them were both post-nesting and all post-rehabilitation loggerhead and green sea turtles. Two turtles migrated >1000 km (1167 and 1254 km; both were post-nesting green turtles), and the remaining 2 migrated >3000 km (3151 and 3481 km; both were post-nesting loggerheads) (Fig. 1a,d, Table 1).

All 7 turtles that migrated 300 km or less travelled along the shoreline, keeping a median distance from shore of 3.652 km (CI: 1.330–5.111 km). Median bottom depth along these migration routes was estimated as 11 m (CI: 3.5–28.4 m). The remaining 4, all heading south-west, alternated between shoreline and open water migration routes. Overall, migrating turtles spent, on average, 78% of the migration phase within 10 km of the shore (range: 10–100%), and on average, 72% of the migration days were spent within this distance from the shore and in shallow waters (50 m bottom depth, or less, range: 7–100%). Several migration routes were shared by different turtles, mostly along the shore, but also in open waters (Fig. 1a,d). Due to the mixed migration strategies, the overall median bottom depth along migration routes and median distance from shore were not significantly different (randomized 1-way ANOVA) from those estimated at foraging or nesting areas.

DISCUSSION

In this study, we identified critical hotspots for nesting, foraging and migration of both green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles in the south-eastern Mediterranean, considerably expanding on previous recent migration data for green (Stokes et al. 2015) and loggerhead turtles (Snape et al. 2016). The shared foraging grounds and migration corridors identified in our study represent the major sea turtle activity regions along south-eastern beaches. We believe that if threats are effectively mitigated in these hotspots, the region's sea turtle population could increase to its formerly high abundance (Hornell 1935, Sella 1981), greatly contributing to the recovery of the entire Mediterranean Sea population because of the high importance of this region to Mediterranean sea turtles.

In the Gulf of Mexico, the loggerhead turtle core home ranges have been estimated to cover from 13 to 335 km² (Hart et al. 2012). Median estimations of the 95% home range in the Atlantic waters of the USA were 1890 and 4372 km² (Hawkes et al. 2011), much

larger than the median (\pm SE) 1092 ± 339 km² foraging home range found in this study. Our findings hint at differences across studies and between breeding and foraging home ranges. Nevertheless, comparison across studies must be treated with caution due to the limitations of home range estimates. Standardization of data is needed to overcome differences in data volume and location accuracies (Börger et al. 2006).

The size of the sea turtles' home ranges varied, as previously observed by Makowski et al. (2006), which is a testament to the resources the region has to offer. As turtles stayed relatively stationary for a long period of time (median \pm SE: 275 ± 63 d), weathering changing temperatures, winter storms and other seasonal challenges, the identified hotspots may offer not only ample, but also varied and sustainable food, as well as suitable hideouts and secure resting sites.

Compared with nesting and migrating behaviors, the tracked turtles offered the most consistent behavior when foraging, with the smallest variation and range in both bottom depth and distance from shore: foraging turtles clearly favor shallow waters, close to shore. As foraging home ranges are primarily restricted by food distribution (Makowski et al. 2006), the movement behavior seen in these turtles most likely indicates benthic feeding, as similarly described in turtles from north Cyprus and Greece (Schofield et al. 2010b).

Over-winter stays at foraging grounds may also be determined by lower sea water temperatures, which lead to reduced metabolism and activity in this season (Hochscheid et al. 2007), contributing to the confined foraging home ranges. Turtles are known to reduce metabolism and food intake, in order to retain fat reserves (Schofield et al. 2010b). This limits migration and overall mobility and is characterized by long dives (Broderick et al. 2007), all suggestive of seasonally reduced activity leading to restricted home ranges.

Due to the small sample size of this study (loggerhead $n = 10$, green $n = 5$), statistical analysis between the 2 species or between sexes was not possible, but suggestive differences were found: green turtles utilized a smaller foraging home range than loggerhead turtles (50% kernel, range: 97.5–230.7 and 104.5–572.5 km², respectively; Table 1), and their bottom depths were shallower (median: 5 and 21 m, respectively) and closer to shore (median: 2.1 and 3.3 km, respectively). This supports the work done by Broderick et al. (2007), who found that green sea turtle fidelity to their foraging grounds is

higher than that of loggerhead sea turtles. Loggerhead sea turtles may use multiple foraging sites (Schofield et al. 2013a), due to differences in their diets. Green sea turtles return to their predictably stable foraging grounds, while loggerhead turtles depend on vagile organisms such as molluscs and crustaceans which are more easily depleted (Broderick et al. 2007); therefore, larger foraging grounds are used.

Nesting season in the eastern and central basins of the Mediterranean extends from mid-May to early-August, peaking from mid-June to mid-July (Levy 2005, Schofield et al. 2013b, Levy et al. 2015). In this study, nesting activity did not capture the early season period because tag deployment was conducted in mid-season and tag longevity was not long enough to capture 2 consecutive nesting seasons. Nevertheless, the habitat utilization documented here was assumed to be roughly the same throughout the season. During the nesting season, turtles inhabited larger areas than when foraging (50% kernel density median: 464 and 137 km², respectively). Although home ranges may seem larger than they actually are due to the accuracy of Argos data, the trend persists. Turtles spent more time in deep waters (median \pm SE: 361 ± 243 m) and further away from the shore (12.159 ± 2.354 km) during the nesting season. Given that the nesting season is much shorter than the foraging period, these observations can only be the result of an active widening of the home range, rather than a sampling artifact. Though the sample size of nesting females was small, which restricted statistical analysis, the sampled turtles showed high consistency in utilizing larger areas in deeper waters. Two main factors may explain this phenomenon: (1) As male turtles have been shown to use home ranges that are half the size of those of females (Schofield et al. 2010b), females might spread out to either find different males to mate with, or rather escape males for occasional rest; (2) reduced food intake during the winter, followed by strenuous migration to breeding sites and a tiring mating season, leave the females in grave need of energy sources. Female turtles, therefore, might feed during the nesting season, as documented in leatherback turtles (Georges et al. 2007, Byrne et al. 2009), as well as loggerheads and green sea turtles in the Mediterranean (Godley et al. 2002, Hays et al. 2002, Schofield et al. 2010b). Given that for most females, nesting sites are not in their usual foraging grounds, larger areas may be needed for them to properly feed. In the deepest ends of their home ranges, females may feed more on pelagic invertebrates (and floating vegetation, in the case of

green turtles), and simply bask on the surface rather than on the bottom to rest (Hays et al. 1999).

When the nesting season was over, nesting females migrated to their foraging grounds. Migration distance and duration varied widely in the tagged green and loggerhead sea turtles, as similarly described in other studies. For example, in north Cyprus, loggerhead sea turtles were found to have migrations that lasted between 6 and 86 d (Snape et al. 2016). In another study from that region, migrations lasted up to 123 d for both loggerhead and green turtles (Broderick et al. 2007), and migrations lasted 6 to 80 d in green turtles in a more widespread regional study of the eastern Mediterranean Sea (Stokes et al. 2015). In our study, a median of 15 ± 27 d (1–86 d) was recorded for post-nesting migration—substantially shorter than the foraging period (8% of all transmission days). These results coincide with the theory that turtles lose body condition during migrations and breeding season at a faster rate than they gain body condition while foraging (Hays et al. 2014b), and thus must spend more time foraging than migrating or breeding. The short migration documented here allows for a long compensation period, even for males, who breed twice as often as females (Hays et al. 2014b) and are likely to migrate to breed more frequently.

Most (64%) of the post-nesting females migrated <300 km. The breeding grounds of these turtles are also frequently used by turtles from other sites in the Mediterranean as foraging grounds (Clusa et al. 2014) and as a migration corridor (Godley et al. 2002, Snape et al. 2016). Slower speed was recorded in the middle migration of a female green sea turtle in the coastal waters of Israel, suggestive of foraging or resting (Rees et al. 2008). It is likely that the southeast Levant Sea conditions enable breeding turtles to decrease migration length or even avoid migration.

Post-nesting migration distances documented in turtles in this study coincide mainly with the lower values of those documented in other Mediterranean sea turtles (Broderick et al. 2007, Schofield et al. 2013a, Stokes et al. 2015, Snape et al. 2016), but were short compared to migration distances seen in the same species in the oceans (Hays & Scott 2013). For example, green turtles migrate 2300 km or more from the Ascension Islands to Brazil (Luschi et al. 1998), and trans-Pacific migrating loggerhead turtles have been reported swimming up to 11 500 km (Nichols et al. 2000). In the Mediterranean Sea, migration ranges for green sea turtles (including nesting sites in Cyprus and Turkey) from 181 to 2641 km have previously been documented (Stokes et al. 2015). In our

study, the migrations ranged from 183 to 1254 km for green sea turtles, and from 87 to 3480 km for loggerheads.

Interestingly, we witnessed a rare short migration (or perhaps better described as residential movement) by a female loggerhead (1 d, 87 km). This behavior has been discovered recently in males that remain residents at or close to (<100 km) the breeding area (Schofield et al. 2013a). Residency in females, however, has been recorded only a few times: in studies on loggerhead turtles in Cyprus (Broderick et al. 2007), and green turtles in the Caribbean (Esteban et al. 2015) and the Galapagos (Seminoff et al. 2008). As increased tracking is revealing more behavioral plasticity (Schofield et al. 2013a), this non-migration strategy may be beneficial to the species in a future where they are likely to face increasing widespread threats, if such resident individuals are protected within safe havens inside relatively small marine protected areas (MPAs) (Almpanidou et al. 2016).

What drives turtles starting from the same breeding sites to use such a varied migration strategy, from residential to long migration? After all, migrating turtles generally cross through suitable foraging grounds on their way to their own foraging grounds (Broderick et al. 2007). Fidelity in green sea turtles may be stronger due to the nutritional benefits of yearly grazed seagrass as well as the predictability of food, while in the omnivorous loggerhead sea turtles, lower fidelity is expected due to the potential depletion of resources in previous feeding bouts (Broderick et al. 2007). Hays et al. (2010) proposed that adult dispersion patterns after breeding may reflect their previous drift scenarios as hatchlings, suggesting that the route taken by adult sea turtles to and from their foraging grounds is influenced by the previous benefits of that route to the juvenile turtles.

Habitat size, shape and location can be critically influenced by environmental parameters and habitat availability (Parnell et al. 2006, Schofield et al. 2010b). In this study, turtles shared migratory routes, foraging grounds and some of their inter-nesting home ranges, reflecting the results of Schofield et al. (2010b). In general, however, the tracked turtle distribution was scattered widely along the coasts, with partial overlap between habitats and a few distinctive shared foraging grounds. The most important foraging areas for Mediterranean loggerheads are now understood to be in neritic waters, and 1 of the major 5 areas is off the Nile Delta in Egypt (Schofield et al. 2013a, Snape et al. 2016). This area is also used by migrating turtles to forage or rest (Rees et al. 2008,

Stokes et al. 2015, Snape et al. 2016). The geographical conditions on the north-eastern African wide and shallow neritic shelf, combined with the high sea surface temperatures found there (Schofield et al. 2013a, Rilov 2016), create ideal sea turtle foraging grounds. Furthermore, the sandy coasts in Israel (Mazor et al. 2013) and Egypt created by Nile Delta sands are highly suitable for nesting, and the region has been a major rookery in the past. However, due to historic intensive fishing and other human-driven threats both then and now (Nada & Casale 2011, Levy et al. 2015), the sea turtle population has dramatically declined. Clearly, the south-eastern Levant coastal waters and beach conditions provide high carrying capacity for sea turtles, as evidenced by historical records. The importance of the region as a multifunctional habitat for adult sea turtles is highlighted by this study. Of course, there are still knowledge gaps to be filled, including pre-nesting migration, mating, survival probabilities for different turtle age categories, activities, and habitat characteristics and use, as well as more migration corridors. In addition, further research is needed to better evaluate the effectiveness of conservation management policies designed to increase sea turtle populations in the region. The conclusions of this study offer guidance for future marine management decisions by providing accurate spatiotemporal data of how sea turtles use this region. Using this information, we can better protect this remaining population, once part of a major Mediterranean sea turtle rookery (Levy et al. 2015), which will allow the Levant sea turtle population to re-flourish.

Conservation policy recommendations

The tracked turtles spent most of their time in their foraging grounds, when not nesting. Because of the relatively large size of most of these foraging grounds, large nature reserves and MPAs are recommended to protect sea turtles and their habitat. In general, MPAs should extend from shallow waters at the coast down to 50 m in depth, and extend at least 5 km from the coast. If, due to non-conservation related constraints, protected areas must be smaller than these guidelines, then the minimum recommended bottom depths and distances from shore can be derived using the foraging home range confidence intervals (CI: 10–24 m and 2.1–4.2 km, respectively).

Using Israel as a case study (Fig. 4), it is recommended that the new insights derived from this

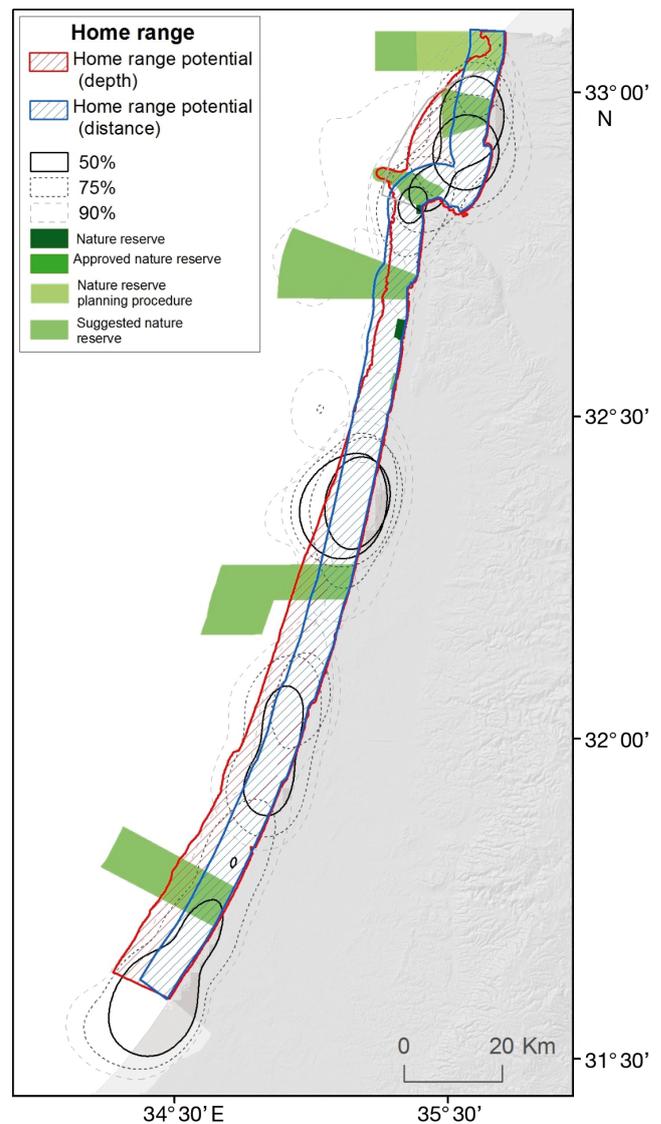


Fig. 4. Nature reserve status (1143 km²), loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtle home range, and the potential home range by distance from shore (1062 km²) and depth (1487 km²), derived from this study

study are taken into account when planning future reserves. Out of all the existing and planned marine nature reserves (1143 km² total protected area), less than 20% (221 km²) and 35% (404 km²) coincides with potential foraging home ranges, characterized by distance from shore and depth of water, respectively.

The turtles' widespread home ranges, of ~2000 km² per individual during the reproduction season, in water 100s of meters deep and dozens of km away from the shoreline, emphasizes the need for dramatic conservation action. Not only do specific nature

reserves and MPAs need to be declared, but human activity needs to be carefully reconsidered and curtailed during the reproduction season (early April to early June; Schofield et al. 2010b) and inter-nesting season (mid-May to early August; Levy 2005). This includes fishing activities, the development of maritime facilities and industries, artificial shock wave blasts (Nelms et al. 2016) and any other sound and light pollution during these times.

Similarly, restrictions on fishing activities (especially fishing with trawlers, gill nets and long lines), seismic surveys and the development of maritime facilities and industries along the migration corridors during the peak migration periods (February to April from foraging to breeding sites, Schofield et al. 2013b, and July to November from breeding to foraging sites) should be considered. Applying these conservation recommendations will not only strengthen the turtle populations, but also be beneficial to the entire marine ecosystem. Future research can continue to help us pinpoint which areas are most valuable to the regional sea turtle populations, but we encourage policymakers to consider the implications of their actions for sea turtle recovery in the meantime. This study provides clear evidence of the importance of these areas to sea turtles and offers conservation recommendations for inclusion in the policy decision-making process.

CONCLUSION

The findings of this study will be useful in guiding future policy decisions. Today, sea turtle populations are facing new threats due to activities in the fields of oil and gas exploration, communications, energy and other maritime infrastructures (Nelms et al. 2016); these impacts are yet to be properly studied. At the same time, sea turtles also face better-understood threats such as fishing and pollution. The relatively localized results of this spatiotemporal analysis of turtle habitat usage in the region offers guidance that can be used to more effectively protect the adults of these species through adaptive management strategies (Broderick et al. 2007), determination of priority habitats, declaration of nature reserves and MPAs, and the restriction of fishery and industrial activities during certain times and geographical areas. The conservation tools that can be derived from this study will help to mitigate sea turtle threats in one of their highest-threat regions in the world (Wallace et al. 2010, 2011, Casale 2011, Levy et al. 2015, Rees et al. 2016).

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