



Evaluating the importance of Marine Protected Areas for the conservation of hawksbill turtles *Eretmochelys imbricata* nesting in the Dominican Republic

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ABSTRACT: Understanding spatial and temporal habitat-use patterns to protect both foraging and breeding grounds of species of concern is crucial for successful conservation. Saona Island in Del Este National Park (DENP), south-eastern Dominican Republic (DR), hosts the only major hawksbill (*Eretmochelys imbricata*) nesting area in the DR (100 nests yr⁻¹, SD = 8.4, range = 93–111), with the population having been critically reduced through hunting. We satellite tracked 9 female hawksbill turtles, and present analyses of their core-use areas with respect to Marine Protected Areas (MPAs) in both their internesting and foraging areas. Kernel utilization distributions indicated that during the internesting period all turtles remained close to their nesting beaches in small home ranges in the territorial waters of the DR, mostly over the continental shelf (<200 m depth). Common core-use areas were located inside the DENP, and 82.7% of all locations were within the DENP. In foraging areas, only 23% of locations were inside MPAs, either in waters of the DR or in waters of the Bahamas, Nicaragua and Honduras. Our results highlight that the protected areas of the DR are vital for hawksbill conservation, and the enforcement of existing legislation governing protected areas in the country is crucial. The present study also corroborates that the waters off Nicaragua and Honduras are exceptionally important foraging areas for hawksbills in the Caribbean, showing the turtle's vulnerability in these waters.

KEY WORDS: Core use areas · Hawksbill turtle · Internesting behaviour · Marine Protected Areas · Satellite tracking

INTRODUCTION

Many marine vertebrate species are of conservation concern as the result of a range of past and ongoing threats (Read et al. 2006, Hoffmann et al. 2011), and the establishment of marine protected areas (MPAs) has been promoted as a key management measure for their conservation (Agardy 1994, Edgar et al. 2014). The management and conserva-

tion effectiveness of MPAs requires full knowledge of the life-history stages of the species they are intended to preserve (Edgar 2011, Scott et al. 2012, Edgar et al. 2014, Mazaris et al. 2014). For highly migratory marine species this means knowledge about their migration routes, as well as the use of their foraging and breeding grounds (Shaffer et al. 2006, Shillinger et al. 2008). Thanks to a revolution in the use of location technologies for tracking the at-

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sea movements of a range of marine species ('biologging'; Hooker et al. 2007, Rutz & Hays 2009, Bograd et al. 2010), we now know a great deal about the movements and behaviour of many marine species and arguably the most about marine turtles (Godley et al. 2008, Hawkes et al. 2011, Maxwell et al. 2011, Pendoley et al. 2014).

The hawksbill turtle *Eretmochelys imbricata* is a marine turtle distributed in tropical and subtropical areas of the Atlantic, Pacific and Indian Oceans and, currently, is listed globally as 'Critically Endangered' by the International Union for Conservation of Nature and Natural Resources (IUCN 2013). In the Caribbean, this species is thought to be a major predator in coral reef ecosystems, with sponges constituting the main component of its diet (Meylan 1988, León & Diez 1999). Numerous studies have suggested the key role of this species in maintaining the structure, ecology and evolution of coral reefs (León & Bjorndal 2002, Bjorndal & Jackson 2003). During the nesting season, which usually spans several months, females return repeatedly to the same beach to lay a variable number of clutches (Allen et al. 2010, Marcovaldi et al. 2012, Walcott et al. 2012, Phillips et al. 2013), similar to that documented for other marine turtle species. However, some populations of marine turtles remain within 100 m of the nesting beaches between nesting attempts (green turtles *Chelonia mydas* on Ascension Island; Hays et al. 1999), while others may travel up to 100 km from the nesting beach to alternative sites (loggerhead turtles *Caretta caretta* in Greece; Schofield et al. 2010). After breeding, and in a similar manner to other marine turtle species (loggerhead turtles: Hawkes et al. 2011, Schofield et al. 2013a; flatback turtles *Natator depressus*: Pendoley et al. 2014), adult hawksbill turtles are then thought to migrate away from the nesting beach to foraging grounds (Meylan et al. 2011). Migratory movements of adult marine turtles, tracked using satellite telemetry, show a broad range of post-nesting migratory strategies, even within studies. These include turtles remaining in waters proximate to the nesting beaches and others migrating to foreign waters many hundreds to thousands of kilometres away (loggerheads: Hawkes et al. 2011, Schofield et al. 2013a; green turtles: Seminoff et al. 2008; hawksbills: van Dam et al. 2008, Horrocks et al. 2011, Hawkes et al. 2012, Moncada et al. 2012).

The Dominican Republic (DR) in the eastern Caribbean hosts regionally significant numbers of nesting hawksbill turtles (Revuelta et al. 2012), but current nesting is largely restricted to protected areas. Saona Island in Del Este National Park

(DENP), south-eastern DR, hosts the last major nesting area in the country (~100 nests yr⁻¹; Revuelta et al. 2012). Although nesting beaches are in a protected area, there has been a marked reduction in the abundance of this species, and egg take is still a major threat at these beaches (Revuelta et al. 2012, 2013).

Here we analyse tracking data from DR nesting hawksbills (building on findings in Hawkes et al. 2012) with respect to (1) behaviour of hawksbill females during the period from the date of attachment at nesting until the final nesting event before departure from the breeding grounds and (2) an assessment of the level of protection afforded to these turtles in their breeding and foraging areas.

MATERIALS AND METHODS

Tagging area

Surveys of nesting hawksbill turtles were carried out in the Jaragua National Park (JNP, south-west DR, 17.816°N, 71.533°W; Fig. 1) and Del Este National Park (DENP, south-eastern DR, 18.807°N, 68.844°W; Fig. 1). Both parks were added to the UNESCO World Heritage list in 2001. JNP covers 1374 km², of which 905 km² comprises coastal and marine areas. Hawksbill turtles nest at the westernmost beaches of the park, Bahía de las Águilas (4.4 km long) and La Cueva (2.5 km). The park receives ca. 20 000 visitors yr⁻¹ (Wielgus et al. 2010). DENP is the second largest coastal national park in the DR, and comprises some of the south-eastern DR and Saona Island (which has an area of ca. 110 km²). The level of protection does not vary across the park. Hawksbill nesting activity is concentrated on 12 sandy beaches (altogether comprising a total of 15 km) interspersed with rocky areas (Revuelta et al. 2013). The adjacent neritic zone is characterized by a wide continental shelf comprising fringing reefs and rocky bottom communities mixed with seagrass beds. Despite the DENP's designation as a national park, the government of the DR allows small-scale artisanal fisheries to exist within its boundaries, mainly for local consumption. However, overfishing has affected the area, with populations of invertebrates (conch and spiny lobster) and reef fish becoming highly depleted (Chiappone et al. 2000). In addition, Saona Island is one of the most popular tourist destinations in the DR, with up to 1000 visitors a day (MacLeod 2001), resulting in heavy motor boat traffic, especially off the west of the island.

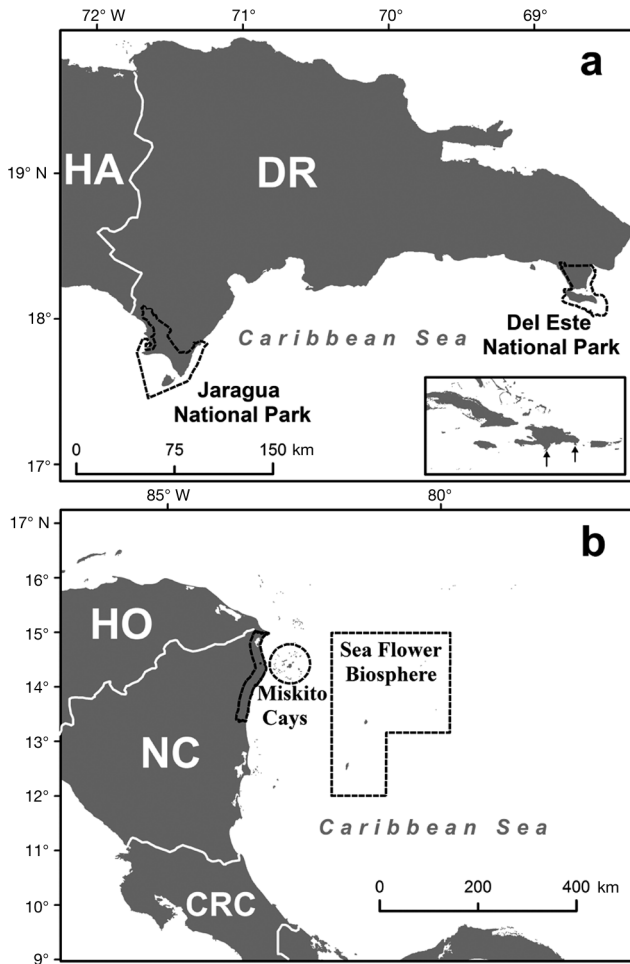


Fig. 1. Study area. (a) Map of the Dominican Republic (DR) indicating hawksbill (*Eretmochelys imbricata*) nesting and foraging areas in protected areas of Jaragua National Park (JNP; south-west DR) and Del Este National Park (DENP; south-east DR, including Saona Island) where turtles were tagged. (b) Hawksbill foraging areas in the western Caribbean. Boundary lines for marine protected areas in the Caribbean Sea are shown. HA: Haiti; HO: Honduras; NC: Nicaragua; CRC: Costa Rica

Marine turtle tracking and satellite data filtering

We attached satellite transmitters to a total of 9 nesting hawksbill turtles, 8 on Saona Island in August–September 2008 and September–December 2009; and 1 (Ei8) in JNP in September 2009. Turtles ranged in size from 81.0 to 94.0 cm curved carapace length (CCL; mean \pm SD: 87.3 ± 4.4 cm; Table 1). None of these turtles had previous transmitters of any type. Transmitters were Wildlife Computers SPOT5 tags ($n = 5$) and Sirtrack Kiwisat 101 tags ($n = 4$) and were set to transmit whenever they were at the sea surface, i.e. a duty cycle of 100% on. To

attach the units, we detained each turtle inside a portable wooden ‘corral’ following nesting or nesting attempts, intercepting them on their way back to the sea. The carapace of each turtle was prepared by scrubbing to remove epibionts and sand and cleaning with acetone. The units were attached to the second vertebral scute of the carapace with 2-part epoxy and covered with a layer of anti-fouling paint (Blumenthal et al. 2006). Before attaching the transmitter, each turtle was measured (CCL) and tagged with small metal Inconel tags to the front flippers. Once tagging was complete we removed the corral, allowing the turtle to return to the sea.

For all transmitters, data were downloaded from the ARGOS satellite system and subsequently analysed with the satellite tracking and analysis tool (STAT; Coyne & Godley 2005) to archive and filter location data. For each reported location, ARGOS calculates a measure of accuracy using 6 ‘location classes’ (LC): 3, 2, 1, 0, A and B. ARGOS assigns accuracy estimates of <250 m for LC3, 250 to <500 m for LC2, 500 to <1500 m for LC1 and >1500 m for LC0 (CLS 2011). As in previous hawksbill telemetry studies (Cuevas et al. 2008, Gaos et al. 2012), the majority of our LCs were categorized as B (ARGOS does not provide estimated errors for LC A or B); thus, we considered the positions LC3, LC2, LC1, LCA and LCB to avoid loss of relevant location data (Hays et al. 2001). These LCs were retained and filtered to remove biologically unrealistic speeds ($>5 \text{ km h}^{-1}$; see Luschi et al. 1998), turning angles ($<25^\circ$ were removed) and elevations (>0 m above sea level).

Identifying nesting events

Due to survey limitations (i.e. it was not possible to survey the entire beach area every night), we could not allocate nests to particular females. Similar to methodology used by Rees et al. (2010), Tucker (2010) and Maxwell et al. (2011), in the present study nesting activity was extracted from the tracking data by evaluating the following criteria, classing a nesting event as having occurred when all of the following 4 criteria were fulfilled: (1) locations were within 1 km of the coastline; (2) the turtle made directed on-shore movement; (3) movements occurred approximately 2 wk after the last known nesting event (for hawksbill turtles, the ‘internesting period’ [Miller 1997]; the time between 2 subsequent nesting events is thought to be approximately 15 d [Beggs et al. 2007]); and (4) high ARGOS LCs (3, 2 and 1) occurred within a short time span.

Table 1. Summary information of Saona nesting hawksbill (*Eretmochelys imbricata*) behaviour and habitat utilisation during the nesting season. CCL: curved carapace length; IN: internesting; IN tracking duration: defined as time from tagging date until the last internesting location; inferred nesting dates: nesting emergences inferred from satellite-tracking data during the nesting season; IN period: number of days between 2 consecutive nesting events. Turtles Ei3 and Ei9 stopped sending signals during their second nesting season in 2011; thus, we could not estimate time in the IN after the last nest. Turtles Ei4 and Ei8 immediately left coastal waters; therefore, no IN period or clutch frequency could be estimated for these turtles. (-): No data; 0: turtle left Saona the day the transmitter was fitted

Turtle	Transmitter attachment (dd/mm/yy)	CCL (cm)	IN tracking duration (d)	Inferred nesting (dd/mm/yy)	IN period (d) (mean ± SD)	Clutch freq.	Days in IN after last nest	Swim speed (km h ⁻¹) (mean ± SD)	Max. dist. offshore (km)
Ei1	11/08/2008	84	34	15/08/2008 30/08/2008 14/09/2008	15.0 ± 0.0	3	1	1.4 ± 1.2	17
Ei2 ^a	28/08/2008	90	60	16/09/2008 29/09/2008 14/10/2008	14.0 ± 1.4	3	14	1.5 ± 1.3	28
Ei2	-	-	-	-	-	-	-	-	33
Ei3 ^a	29/08/2008	90	48	15/09/2008 30/09/2008 14/10/2008	15.3 ± 1.4	3	1	1.2 ± 1.3	25
Ei3	-	-	52	24/07/2011 10/08/2011	17.0	2	-	0.7 ± 0.8	13
Ei4	19/09/2008	94	0	-	-	-	0	-	-
Ei5	30/09/2008	92	28	15/10/2008	15.0	2	13	2.4 ± 2.7	39
Ei6	27/10/2008	81	51	28/11/2008 14/12/2008	16.0	3	2	1.4 ± 1.6	17
Ei7	01/11/2008	84	37	18/11/2008 03/12/2008	16.0 ± 1.4	3	4	1.4 ± 1.5	16
Ei8	07/08/2009	84	0	-	-	-	0	-	-
Ei9	01/09/2009	87	64	02/07/2011 18/07/2011 02/08/2011 18/08/2011	15.7 ± 0.6	4	-	0.8 ± 1.0	14

^aTurtles tracked during 2 successive nesting seasons

Turtles' core-use areas and distribution within MPAs

To minimize autocorrelation in spatial analysis we generated median daily locations for each turtle from the filtered locations (James et al. 2005). To determine core-use areas, foraging and nesting data were extracted using displacement plots (a plot showing the distance, i.e. displacement, from the release site for each location received from each turtle, over time; see Blumenthal et al. 2006, Hawkes et al. 2012), which allowed them to be differentiated from areas of migratory-use. Home range size was then estimated separately for foraging and nesting periods using minimum convex polygons (MCP), a non-statistical measure which encapsulates the area used by an individual within a polygon formed by joining the outermost sighting positions (Burt 1943). MCP is a simple calculation that allows for comparisons between studies (Hooge et al. 1999), but is unable to describe fine-scale

movements and preferred area used within the polygon. It may also be inflated by inaccurate yet plausible data outside the true area of utilisation (Laver & Kelly 2008). Therefore, core-use areas were identified using fixed kernel density estimation (KDE), with individual kernel contours delineated using a smoothing factor (h) of 1.5 for internesting area (area occupied during nesting season) and 2.5 for foraging grounds (areas where turtles migrate and settle to feed during non-nesting periods). Density distributions were represented on the maps by the 50 and 90% utilisation distribution (UD) contours. We used a 90% KDE to estimate the overall home foraging and internesting home range of a turtle, and a 50% KDE to represent the core area of activity (Powell 2000). For turtles tracked through 2 consecutive nesting seasons, KDE was calculated separately for each nesting season. Following the methodology of Hart et al. (2013) we did not estimate KDEs for turtles that transmitted for <20 d (i.e. had fewer than 20 median daily locations).

Common use areas

Common core-use areas, where multiple turtles spent time during breeding periods, were generated for all turtles combined. These areas were determined by pooling the data of all locations to obtain an overall core area use for all turtles; afterwards we calculated 90 and 50 % KDEs.

To analyse the location of turtles with respect to MPAs, median daily turtle location data were overlaid on the World Database on Protected Areas (www.wdpa.org). Site fidelity was quantified using a residency index (Mason & Lowe 2010), calculated by dividing the number of days a female was detected within the boundaries of an MPA by the number of days the female was monitored (i.e. nesting season and foraging period). Values ranged from 0, indicating no residency, to 1 indicating a high degree of residency. All spatial analyses were carried out in ArcGIS 10 (ESRI 2010). Data are presented as mean values (\pm SD) unless otherwise stated.

RESULTS

Overall transmission success rate (median number of locations received per day per turtle) ranged between 1.8 and 5.6 locations d^{-1} during the nesting season and 1.0 and 4.2 locations d^{-1} in foraging grounds (Table 2). Transmitter duration was variable: Turtle Ei1 was only tracked during the nesting

season; Turtles Ei4 and Ei8 departed immediately following device attachment and were therefore only tracked during the foraging period; the 6 other turtles (Ei2, Ei3, Ei5, Ei6, Ei7 and Ei9) were tracked during both internesting and foraging (Table 2). Transmitters attached to 3 turtles (Ei2, Ei3 and Ei9) functioned for particularly long periods, permitting insight into multi-year space use. These 3 turtles were tracked from arrival at their foraging grounds until their departure to breed and nest again in the DR.

Insight into the nesting season behaviour

We analysed a total of 370 tracking days from the 7 turtles for which we had internesting data (see above). Individual tracking durations during the nesting season ranged from 0 to 64 d (37.4 ± 22.7 d; Table 1). Excluding Turtles Ei4 and Ei8, as well as Turtle Ei9's first nesting season (as it left coastal waters immediately after laying the last clutch), we estimated that hawksbill females migrate from the nesting area 4.3 ± 5.8 d after laying their last clutch of the season (range: 0–14 d; Table 1). Twenty nesting events were inferred from 7 turtles (including 2 turtles that were recorded nesting in 2 different years; Table 1). We estimated time between nesting events ('internesting period'; Miller 1997) of 15.5 ± 0.9 d (range: 14–17 d). Turtles Ei1, Ei2 and Ei3 did not successfully nest at the time of transmitter deployment;

Table 2. Transmission success (mean number of locations received per day [mdl]), Minimum convex polygon (MCP) and kernel density estimation (KDE) for hawksbill turtles *Eretmochelys imbricata* in their internesting and foraging grounds. BH: Bahamas; CO: Colombia; DR: Dominican Republic; HO: Honduras; NC: Nicaragua. Turtle Ei1 stopped transmitting before arriving at the foraging ground. Turtle Ei2 (a, b) was tracked during 2 nesting and foraging seasons. Ei3 was tracked during 2 nesting seasons (a, b) and 1 foraging season (a). Turtles Ei4 and Ei8 departed immediately following device attachment. Turtle Ei5 had fewer than 20 median daily locations (n = 16) during the nesting season for KDE analysis. MCP sizes in foraging grounds also reported in Hawkes et al. (2012). (-): No data available

Turtle	Internesting				Foraging				Maritime boundaries
	mdl	MCP (km ²)	90% KDE (km ²)	50% KDE (km ²)	mdl	MCP (km ²)	90% KDE (km ²)	50% KDE (km ²)	
Ei1	3.1 \pm 2.0	306.4	26.9	11.1	–	–	–	–	–
Ei2a	1.9 \pm 1.8	302.3	28.3	8.7	2.2 \pm 1.4	8124.1	279.1	21.4	NC/HO
Ei2b	–	1101.2	39.0	16.5	–	38.2	14.2	3.4	NC
Ei3a	3.8 \pm 2.6	290.7	31.9	9.3	2.5 \pm 1.5	27001	59.4	12.7	NC/CO
Ei3b	–	68.4	24.0	5.4	–	–	–	–	–
Ei4	–	–	–	–	1.8 \pm 1.2	7033.2	230.1	38.4	NC/HO
Ei5	2.1 \pm 1.8	947.4	–	–	1.0 \pm 1.8	1968.7	57.3	15.6	DR
Ei6	2.3 \pm 1.3	219.8	24.1	13.3	2.0 \pm 1.4	1772.2	29.9	6.9	DR
Ei7	1.8 \pm 1.3	238.1	61.6	24.7	1.3 \pm 1.2	3456.3	65.1	20.3	BH
Ei8	–	–	–	–	2.4 \pm 1.4	416.7	13.1	3.4	HO
Ei9	5.6 \pm 2.7	158.3	60.7	16.4	4.2 \pm 2.0	13219	129.5	23.9	NC/HO

thus, interesting period was determined from the first inferred nesting date instead. Mean minimum clutch frequency of 7 females for which we have records was 2.9 ± 0.6 clutches (range: 2–4 clutches; Table 1).

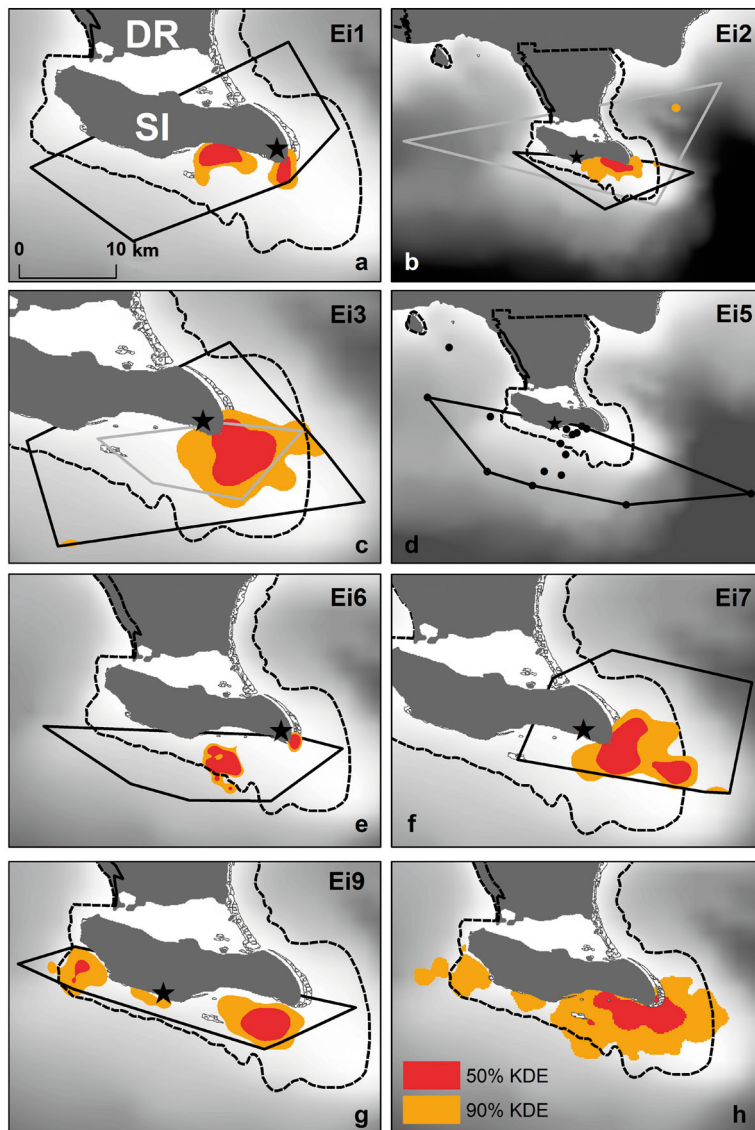


Fig. 2. Individual hawksbill turtle (*Eretmochelys imbricata*) interinteresting areas in Del Este National Park indicated by minimum convex polygons (MCP; solid lines) and 90% (yellow) and 50% (red) utilization distributions (UDs) for (a) Turtle Ei1, (b) Turtle Ei2, (c) Turtle Ei3, (d) Turtle Ei5, (e) Turtle Ei6, (f) Turtle Ei7, (g) Turtle Ei9 and (h) the common core-use area of these 7 turtles tracked during the nesting season identified using 50 and 90% UD. For Turtles Ei2 and Ei3 two MCP areas, 1st nesting season (black polygon) and 2nd nesting season (light gray polygon), are shown. For these 2 turtles 50 and 90% KDEs include locations for the 2 nesting seasons recorded. DR: Dominican Republic. SI: Saona Island. Coral reef ecosystems are indicated by light gray outlines, and marine protected areas, by dashed black lines. Dark gray: land mass; white to black: bathymetry; stars: tagging locations

During the nesting season, all turtles remained in the territorial waters of the Dominican Republic, mostly over the continental shelf (<200 m depth; Fig. 2). Turtles spent most of their time in areas characterized by relatively shallow waters, with KDE 50% for all turtles over water <100 m deep (64.4 ± 22.8 m). Turtles Ei2 and Ei5 made excursions beyond the shelf (e.g. to the 1000 m isobath; Fig. 2b,d). Turtles were usually located 1.4 to 4.3 km from the coast (SD range: 2.1–5.7 km), and mean maximum distance from the coast was 22.4 ± 9.2 km (range: 13–39 km; Table 1). Analyses of the turtles' daily locations showed that during the nesting season, of the 370 total tracking days, 306 (82.7%) were within the borders of the DENP. The turtle's residency index (calculated for turtles with >20 d of data, i.e. excluding Turtle Ei5) ranged from 0.65 to 1.0 (0.84 ± 0.1), indicating a high degree of use of the protected area.

Core-use interesting areas

We calculated MCPs for 7 turtles, 2 of which (Turtles Ei2 and Ei3) transmitted data for a second nesting season, resulting in 9 MCPs (Table 2, Fig. 2). Interinteresting areas occupied by the turtles ranged from 68.4 to 1101.2 km² (403.6 ± 362.0 ; Table 2). The 90% KDEs ($n = 8$) for the 6 turtles for which nesting season core areas were calculated were much smaller and ranged from 24.0 to 61.6 km² (37.1 ± 15.6 km²; Table 2), and the mean 50% KDEs area was 13.2 ± 6.0 km² (5.4 to 24.7 km²; Table 2). With the exception of Turtle Ei2, there was no substantive variation in home range size among the 7 hawksbill turtles tracked during their nesting season (Fig. 3), with large portions of MCPs and KDE overlapping (Fig. 2). Turtles Ei2 and Ei3 occupied similarly sized areas in the same locations during their 2 tracked nesting seasons (Fig. 2b,c). There were no correlations between turtle size and duration of the nesting season (Pearson's $t = -0.7$, $df = 5$, $p = 0.5$) or between turtle size and the nesting season area (Pearson's $t = -1.02$, $df = 5$, $p = 0.3$).

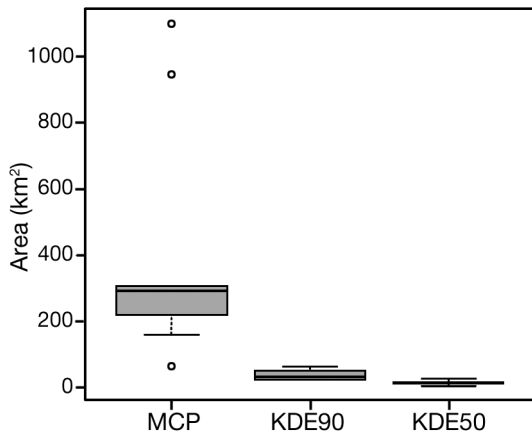


Fig. 3. Home range size of the 7 hawksbill turtles *Eretmochelys imbricata* tracked during their nesting season in the Dominican Republic, measured using Minimum Convex Polygons (MCP), Kernel Density Estimates of 90% of the core range (KDE90) and 50% of the core range (KDE50). Boxes show inter-quartile range, black horizontal line shows median values, whiskers show range. Outliers (for MCP) are shown as white circles and are for Turtle Ei2 (see 'Materials and methods' for descriptions)

Common core-use areas

The interesting common use area 90% and 50% KDEs were 212.2 and 37.9 km², respectively (Fig. 2h). This common use area was situated on coral reefs at the easternmost tip of the island, and the individual home ranges for all 7 turtles overlapped, across turtles and years. Overall, the common core-use area during nesting was situated inside the DENP's boundaries (Fig. 2h). Generally speaking, the home ranges of turtles during their foraging periods (Fig. 4a) did not overlap with one another. However, 1 individual was tracked through 2 consecutive years and was tracked returning to the same foraging area (Fig. 4f).

Foraging areas and MPAs

Foraging areas of 5 females (Ei2, Ei3, Ei4, Ei8, Ei9) were located along the waters off Honduras and Nicaragua (Fig. 4a). In those waters there are 2 main protected areas, the Miskito Cays and the Seaflower MPA (part of the Seaflower Biosphere

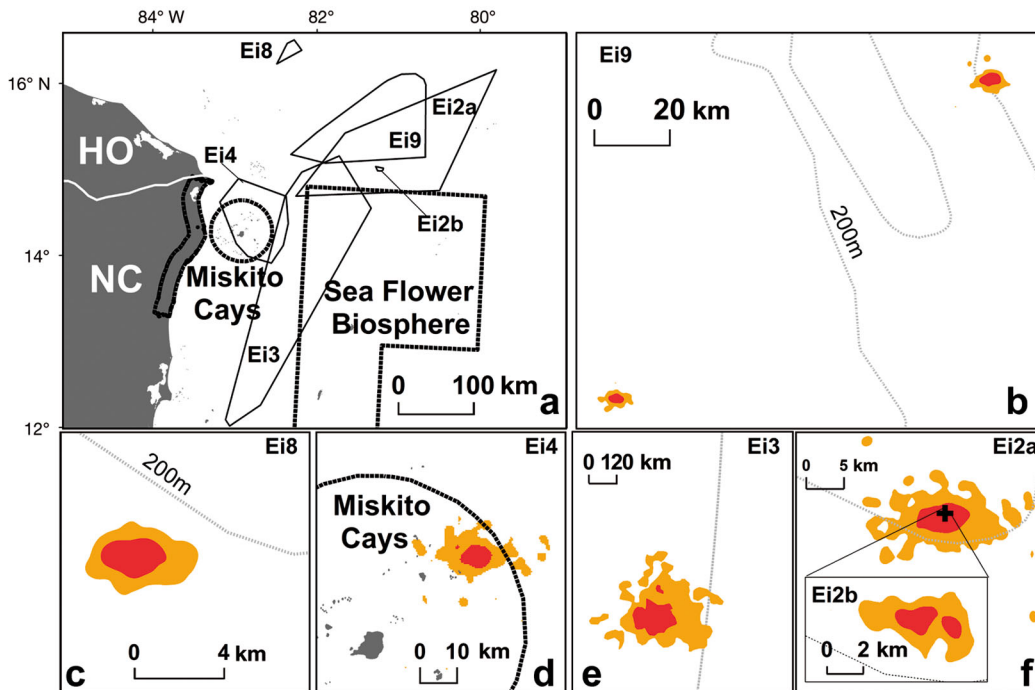


Fig. 4. (a) Minimum convex polygons (MCP; solid lines) of hawksbill turtles *Eretmochelys imbricata* at foraging areas off Nicaragua (NC) and Honduras (HO). The MCP of Turtle Ei2b shows the 2012 foraging period. The marine protected areas Miskito Cays and Seaflower (dashed black lines) are shown. Core-use areas defined by 90% (yellow) and 50% (red) utilisation distributions (UDs) for (b) Turtle Ei9 which occupied 2 separate areas during the same foraging period, (c) Turtle Ei8, (d) Turtle Ei4, (e) Turtle Ei3 and (f) Turtle Ei2: Ei2a shows the foraging period in 2008, the first year this turtle was observed; Ei2b (+, inset) shows the same turtle occupying the same area in 2012, the second year it was observed. Note different scales. Dashed light grey line: 200 m bathymetric contour

Reserve, belonging to Colombia). The Miskito Cays (27 km²) is an archipelago located offshore along the north-eastern Caribbean coast of Nicaragua (Fig. 1). The seagrass beds and reefs in the cays are among the Atlantic's greatest foraging grounds for green (*Chelonia mydas*) and hawksbill marine turtles (Bjørndal & Bolten 2003). The Seaflower MPA, located in the south-western Caribbean Sea (Fig. 1) is the largest MPA in the wider Caribbean (65 000 km²), protecting mangroves, seagrass beds and the largest and most productive coral reefs in the region (Taylor et al. 2013). With the exception of Turtles Ei3 and Ei4, with residency indexes of 0.02 and 0.91, respectively (Seaflower Biosphere Reserve and Miskitos Cays, respectively), the turtles were not located in protected waters for any of their tracked foraging period (Fig. 4a–f). After nesting at Saona, Turtles Ei5 and Ei6 remained in DR waters within coastal reef ecosystems (Fig. 5a,b). Turtle Ei5 remained inside the JNP (residency index: 0.91; Fig. 5b). Turtle Ei6's foraging area was located in the waters adjacent to Bahía de las Calderas (southern DR coast) outside of MPAs (Fig. 5a). Turtle Ei7 travelled north-westward to the Bahamas, where its core-use area was not in protected waters (Fig. 5c).

DISCUSSION

The present study has highlighted space-use patterns for endangered hawksbill turtles in the DR, demonstrating some key novel findings for the population and providing support for key conservation recommendations.

Interesting behaviour

Nesting hawksbills from Saona Island remained in the waters adjacent to their nesting beaches, using small home range areas during interesting periods. Core activity areas occurred in shallow waters (<200 m) and were associated with coral reefs. Our results support previously described hawksbill interesting spatial behaviour observed in other interesting areas throughout the Caribbean (van Dam et al. 2008, Marcovaldi et al. 2012, Walcott et al. 2012). Although we did not record diving depth, it appears turtles were likely to have been making shallow dives; indeed, hawksbill turtles probably exhibit shallow diving behaviour throughout the year (Storch et al. 2005, Blumenthal et al. 2009). Regardless of the nesting location on the beach, core-use

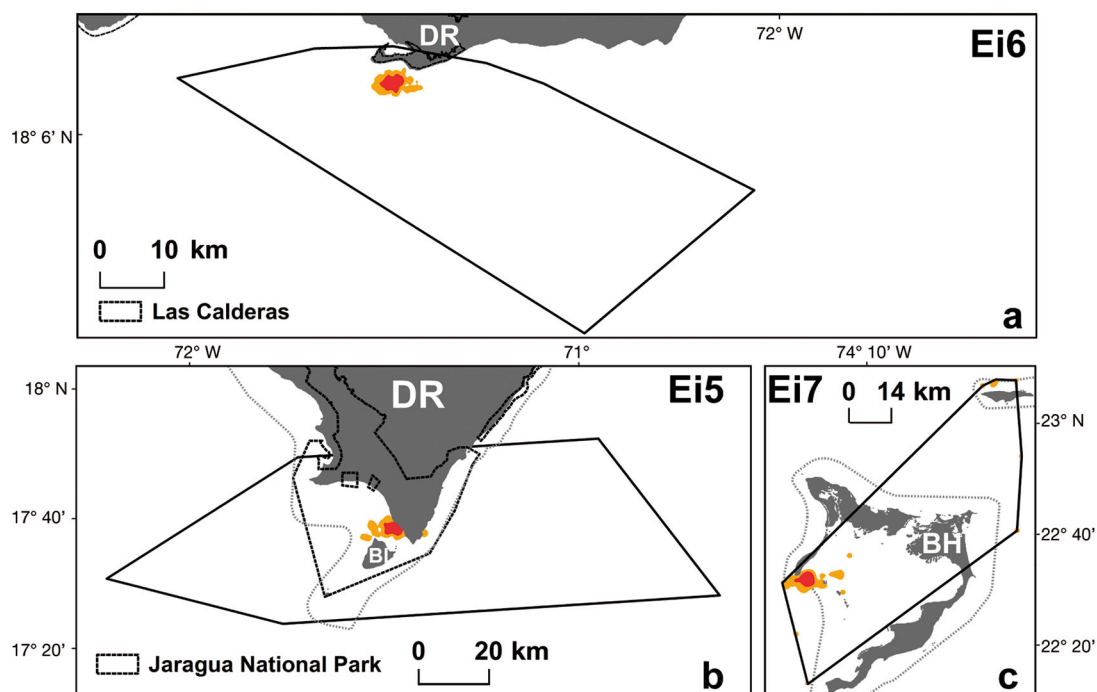


Fig. 5. *Eretmochelys imbricata*. Foraging core-use areas defined by minimum convex polygons and 90% (yellow) and 50% (red) utilisation distributions of (a) Turtle Ei6 near Las Calderas Natural Monument (south Dominican Republic); (b) Turtle Ei5 in waters inside Jaragua National Park boundaries (south-west DR; BI: Beata Island) and (c) Turtle Ei7 in waters of the Bahamas (BH). Note different scales. Dashed light grey line: 200 m bathymetric contour

areas were situated on coral reefs at the eastern-most tip of the island. Turtle preference for particular interesting areas has been related to adequate resources and the quality of the habitat occupied (Hart et al. 2010). The abundance of fringing reef systems inside DENP's marine area likely accounts for hawksbill turtle affinity for this area. The abundance of sheltered resting sites (e.g. ledges and caves in coral reefs) could be an important resource, helping nesting females to preserve energy during their reproductive period (Houghton et al. 2008, Hart et al. 2010).

Nesting season activity patterns for Saona hawksbill turtles were similar to results for hawksbill turtles satellite tracked during the nesting season elsewhere. However, it should be noted that tagging date was the only confirmed nesting event; hence, nesting dates were inferred by turtle tracks (see 'Materials and methods' section), and nesting dates and interesting periods were approximated. Our estimated interesting period (mean: 15.5 ± 0.9 d; range: 14–17 d) was similar to ranges reported elsewhere (14–17 d; Barbados: Beggs et al. 2007; Mona Island: van Dam et al. 2008). Tracking-derived minimum clutch frequency ranged from 2 to 4 clutches, which is in accordance with conspecifics elsewhere (Witzell 1983). Saona turtles remained in the interesting area for only a few days following their final nesting event, supporting the hypothesis that hawksbill turtles may not forage during the nesting season, as has been proposed in other studies (e.g. van Dam et al. 2008).

Core-use areas and MPAs

Home range estimations provide knowledge of marine turtles' core areas of activity, underscoring hotspots for their protection (Scott et al. 2012, Schofield et al. 2013b, Pendoley et al. 2014). The results of the present study highlight that effective protection of reproductively active hawksbill turtles in the DR can most effectively take place within the waters of the DR itself. It should be noted that the number of tracked turtles studied in the present paper represents ca. 40% of the total annual nesting stock in the DR (Revuelta et al. 2012), so results may be representative of the entire population nesting in the DR.

Our results also reveal that, during their nesting season, hawksbill turtles from Saona Island remain mostly within the maritime limits of the DENP MPA. Although the DENP MPA in theory offers protection

for this Critically Endangered species, in reality turtles face multiple anthropogenic threats inside the park.

Firstly, the expansion of tourism has increased the boat traffic around Saona Island, particularly in the west part, and has also increased the pressure on coral reefs from direct pollution (Wilkinson 2000). Secondly, artisanal fishermen have essentially uncontrolled access to the park, resulting in the depletion of large reef fish, conch and lobster populations (Chiappone et al. 2000). Finally, illegal capture of adult turtles by fisherman has also been documented (Revuelta et al. 2013).

Hawksbill turtles satellite tracked from Saona show a range of migratory strategies, with some turtles remaining near nesting sites in the DR waters and others migrating to international foraging grounds (Hawkes et al. 2012). This flexibility in migratory routes and foraging-area destinations has previously been reported for nesting populations of different species of marine turtles, e.g. green turtles in the Galapagos (Seminoff et al. 2008), loggerhead turtles in Greece (Hays et al. 2010) and flatback turtles in Australia (Pendoley et al. 2014). Most of the turtles that migrated internationally foraged in waters off Nicaragua and Honduras ($n = 5$), which has already been confirmed as a preferred foraging ground for hawksbills nesting in other Caribbean areas, such as Costa Rica, the eastern Caribbean and Cuba (Troëng et al. 2005, Horrocks et al. 2011, Moncada et al. 2012), and also for other marine turtle species nesting in the Caribbean region (loggerhead: Masuda 2010; green turtle: Vander Zanden et al. 2013). While turtles were located within MPAs during the nesting season, at their foraging grounds they were mostly (78.0% of total foraging days tracked) outside of any MPA. Of the 5 tracked turtles just one (Turtle Ei4) spent a large proportion of the time inside a protected area (Miskito Cays). However, the effectiveness of the protection in this area is questionable since legal and illegal marine turtle fisheries continue to exist (Bräutigam & Eckert 2006). The lack of protection in the waters off Nicaragua and Honduras, thus, poses a potentially significant conservation problem, not only for many Caribbean hawksbill nesting populations, but also for other marine species. In the Bahamas, there are 8 marine national parks, and direct harvest of marine turtles is probably considerably less common. However, protected waters make up a small portion of the 630 000 km² exclusive economic zone of the Bahamas (<1%), and, thus, it is not surprising that the turtle foraging here did so outside of protected areas.

Turtle Ei5 stayed in DR waters, spending most of the time (91% of the total days tracked) within JNP maritime limits, which supports previous studies about the importance of this area for marine turtle conservation for the country, not only as a foraging ground for juveniles and adults, but also as a nesting area (León & Diez 1999, Revuelta et al. 2012). The second potential foraging ground in the DR was located in waters adjacent to the Natural Monument Bahía de Calderas along the south coast of the country. This protected area encompasses around 15 km of sand dunes, but does not yet incorporate the sea. Sporadic nesting by *Chelonia mydas* has also been detected on these beaches (Y. M. León pers. obs.). Despite the evident importance of this area for biodiversity conservation, and its protected status, it is threatened by the extraction of sand for commercial purposes and illegal construction by the hotel industry, as well as indiscriminate fishing activities (Perdomo et al. 2010). Such lack of enforcement of conservation actions in protected areas hinders the effective protection of these critical habitats for marine turtles and is an urgent target for improved conservation.

Conclusions and conservation recommendations

In this study, we described DR hawksbill nesting turtles' use of MPAs at nesting and feeding grounds, adding information to the use of MPAs by this species in the Caribbean region. This information highlights the significance of protected areas in the DR for interesting and foraging hawksbills, showing the need to enforce existing legislation of the protected areas in the country. Hawksbill turtles use waters inside the protected areas of DENP and JNP year-round, areas that are severely threatened by human activities. Hence, efforts must be increased to mitigate illegal fishing in the waters of these parks. In the case of waters around Saona, we recommend the creation of a near-shore zone of maximum protection that would enhance the protection of the rookery in this heavily used area (i.e. by restricting the boat traffic in this zone). Likewise, we propose the expansion of Las Calderas Natural Monument boundaries offshore, due to its importance, not only for turtles, but also for other species and ecosystems. The present study also supports that the waters off Nicaragua and Honduras are exceptionally important foraging areas for hawksbills in the Caribbean. These grounds overlap with those identified for other endangered species, strengthening the importance of protecting

them. We highly recommend that the MPAs set up for marine turtle conservation in this region are re-assessed. In line with the recommendations made by Edgar et al. (2014), implementation of no-fishing zones, an increase in the level of compliance and the extension of boundaries would enhance the effectiveness of MPAs and help secure marine biodiversity.

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