



# Post-breeding migration routes of marine turtles from Bonaire and Klein Bonaire, Caribbean Netherlands

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**ABSTRACT:** The management of small rookeries is key to conserving the regional genetic diversity of marine turtle populations and requires knowledge on population connectivity between breeding and foraging areas. To elucidate the geographic scope of the populations of marine turtles breeding at Bonaire and Klein Bonaire (Caribbean Netherlands) we examined the post-breeding migratory behavior of 5 female loggerheads *Caretta caretta*, 4 female green turtles *Chelonia mydas*, and 2 male and 13 female hawksbill turtles *Eretmochelys imbricata* during the years 2004–2013. After leaving Bonaire, the 24 tracked turtles frequented foraging grounds in 10 countries. The distances swum from Bonaire to the foraging areas ranged from 608 to 1766 km for loggerhead turtles, 198 to 3135 km for green turtles, and 197 to 3135 km for hawksbill turtles, together crossing the waters of 19 countries. Males represented the minority in this study, but we made 2 key observations that require further research: males remained in the vicinity of the breeding area for 3–5 mo, which is 2–5 times longer than females, and males migrated greater distances than previously recorded. Although the turtles dispersed widely across the Caribbean, there appeared to be 2 benthic foraging areas of particular importance to all 3 species of marine turtles breeding at Bonaire, namely the shallow banks east of Nicaragua and Honduras (n = 8 tracked turtles) and Los Roques, Venezuela (n = 3). Marine turtles breeding at Bonaire face threats from legal turtle harvesting, illegal take, and bycatch in the waters that they traverse across the Caribbean.

**KEY WORDS:** *Chelonia mydas* · *Caretta caretta* · *Eretmochelys imbricata* · Migration · Foraging areas · Population connectivity · Satellite telemetry

## INTRODUCTION

It is by now well established that marine turtles can migrate long distances between their breeding areas and foraging grounds (Hays & Scott 2013). However, for small rookeries, such as those utilizing the islands of the Caribbean Netherlands, knowledge of turtle migratory behavior remains scarce. The beaches and near shore areas of Bonaire and Klein Bonaire, Car-

ibbean Netherlands, are used regularly for breeding by 3 marine turtle species: loggerheads *Caretta caretta*, green turtles *Chelonia mydas* and hawksbills *Eretmochelys imbricata*. Klein Bonaire beaches harbor the highest concentration of nesting hawksbill and loggerhead turtles in the southern Caribbean (excluding Panama) (Debrot et al. 2005, Dow Piniak & Eckert 2011). Post-breeding adult turtles do not appear to remain near the islands after the reproduc-

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tive season (Stapleton et al. 2014), yet it is unknown what their migration routes are and to which foraging grounds these adults migrate.

All marine turtles have been legally protected on and around the islands since 1991. Klein Bonaire, the most important nesting area, received full protection from development when it was purchased by the government in 1999 and incorporated in its entirety into the Bonaire National Marine Park. In order to set up biologically sound management strategies, comprehensive baseline knowledge is required on turtle migration in the Dutch Caribbean. There is, however, a significant lack of knowledge on the migration routes of post-breeding adults and on how nesting colonies from Bonaire are linked to regional neritic foraging aggregations. Knowledge of such linkages is valuable, as foraging aggregations are not homogeneously distributed across the Caribbean Sea and migration routes can vary among individuals of the same nesting colony (e.g. Bowen et al. 2007). Biogeographical information on migratory behavior is therefore required for prioritizing research and conservation efforts, for example, in the assignment of Regional Management Units (Godley et al. 2008, Hamann et al. 2010, Wallace et al. 2010).

In order to identify migration routes and key neritic foraging habitats, we used satellite telemetry to track the movements of marine turtles after breeding at Bonaire and Klein Bonaire. Our specific aims were to (1) identify current post-breeding migration routes with the aid of satellite tracking and (2) establish the location of neritic foraging grounds of breeding populations at Bonaire.

## MATERIALS AND METHODS

This study was carried out during the period 2003–2013 in the marine turtle breeding areas at Bonaire and Klein Bonaire: No Name Beach on Klein Bonaire (12.0953° N, 68.1756° W), Playa Chikitu on NE Bonaire (12.1650° N, 68.20540° W), and South Bonaire (12.0233° N, 68.1557° W). Since the year 2010 Bonaire has formally been part of the Caribbean Netherlands as a special municipality ('Bijzondere Gemeente') of The Netherlands. As a signatory of diverse international treaties (e.g. Cartagena/Specially Protected Areas and Wildlife [SPAW] protocol, Convention on Biological Diversity, CITES Convention, Convention for Migratory Species, Inter-American Convention for the Protection and Conservation of Sea Turtles), The Netherlands is obliged to protect marine turtles inhabiting Dutch Caribbean waters.

For the 3 species (loggerhead, green and hawksbill turtles) combined, the breeding season spans the period from May to December, with a peak in nesting between July and September (Stapleton et al. 2014). Turtles were selected based on their size (straight carapace length > 80 cm). Further behavioral observations and recapture data on tagged individuals showed that the tracked turtles can be considered 'breeding turtles'; females emerged on nesting beaches of Bonaire and tagged males were mating, as observed during in-water surveys. Additionally, mature-size turtles were not observed during in-water surveys outside the breeding season in Bonaire's waters (Stapleton et al. 2014).

Breeding turtles were held for tagging, measurement, and transmitter application on nesting beaches (14 females, after oviposition) or in waters immediately adjacent to the beaches (3 female loggerheads, 2 female hawksbills, 2 male hawksbills) (see Table 1, Fig. 1A). All animals in this study were double-tagged on their front flippers using metal Inconel No. 681 flipper tags ([www.nationalband.com](http://www.nationalband.com)) and their lengths were measured (straight [SCL] or curved [CCL] carapace length taken from the nuchal notch to the posterior tip of the longest post-central scute). Turtles were kept on the beach in a custom-built box or, at sea, constrained in a small boat. Satellite transmitters used were the models ST-20 (size: 12 × 6 × 3 cm; weight in air: 280 g; Telonics), Spot4 (mold203: size: 16 × 4 × 3 cm; weight in air: 260 g; Wildlife Computers), or Spot5 (size: 8 × 5 × 2 cm; weight in air: 95 g). Prior to transmitter attachment the carapace was cleaned by removing external commensals, then the instrument was applied at the highest point on the carapace using a silicone or latex elastomer base and covered with resined fiberglass, following Balazs et al. (1996). A fiberglass reinforcement strip was placed anterior to the point of antenna attachment to reduce abrasion to the antenna. An angled piece of fiberglass was positioned anterior to the flat frontal area of the ST-20 transmitters to reduce hydrodynamic drag. Turtles were released at the location of capture (recorded by GPS) after the 2–4 h transmitter application procedure. In subsequent years, whenever possible, study animals were recaptured, and, if transmitters remained attached, these were removed (n = 3). Location data for instrumented turtles were received through Argos. Studies by Argos (2013) and Hays et al. (2001, 2014) have shown that Argos Location Classes (LC) 3, 2, 1 are the most reliable; thus, data in LCs 0, A, and B were removed prior to the plotting of tracks. Locations (n = 134) were filtered to exclude biologically unreasonable results for travel speeds

$>5 \text{ km h}^{-1}$  (Luschi et al. 1998, 2001, Seminoff et al. 2008). As post-breeding turtles were not travelling in straight lines on post-nesting migrations, but rather were expected to be moving in complex ways in coastal waters, we did not use a turning angle filter. Final maps were produced with QGIS software (QGIS Development Team 2015). Minimum turtle migration track length was measured by examining the total path connecting all coordinates with Argos LCs 1, 2, and 3. Date of departure from the breeding grounds was the date when a distance post-breeding  $>20 \text{ km}$  from the transmitter application location was attained and the turtle exhibited sustained departure momentum (Blumenthal et al. 2006, Hawkes et al. 2012). Date of arrival at the foraging grounds was deter-

mined by the first occasion of the animal reaching an area  $<20 \text{ km}$  in radius, wherein later LC 1, 2, and 3 positions were located during a period of 7 d or longer. The location was subsequently evaluated to be a foraging site based on the literature, ground-truthing (Puerto Rico), or the assessment of habitat and depth from remote sources (e.g. maps, Google Earth).

## RESULTS

A total of 24 turtles were tracked; all migrated to foraging grounds outside the Exclusive Economic Zone (EEZ) of Bonaire (Fig. 1). In total the turtles tra-

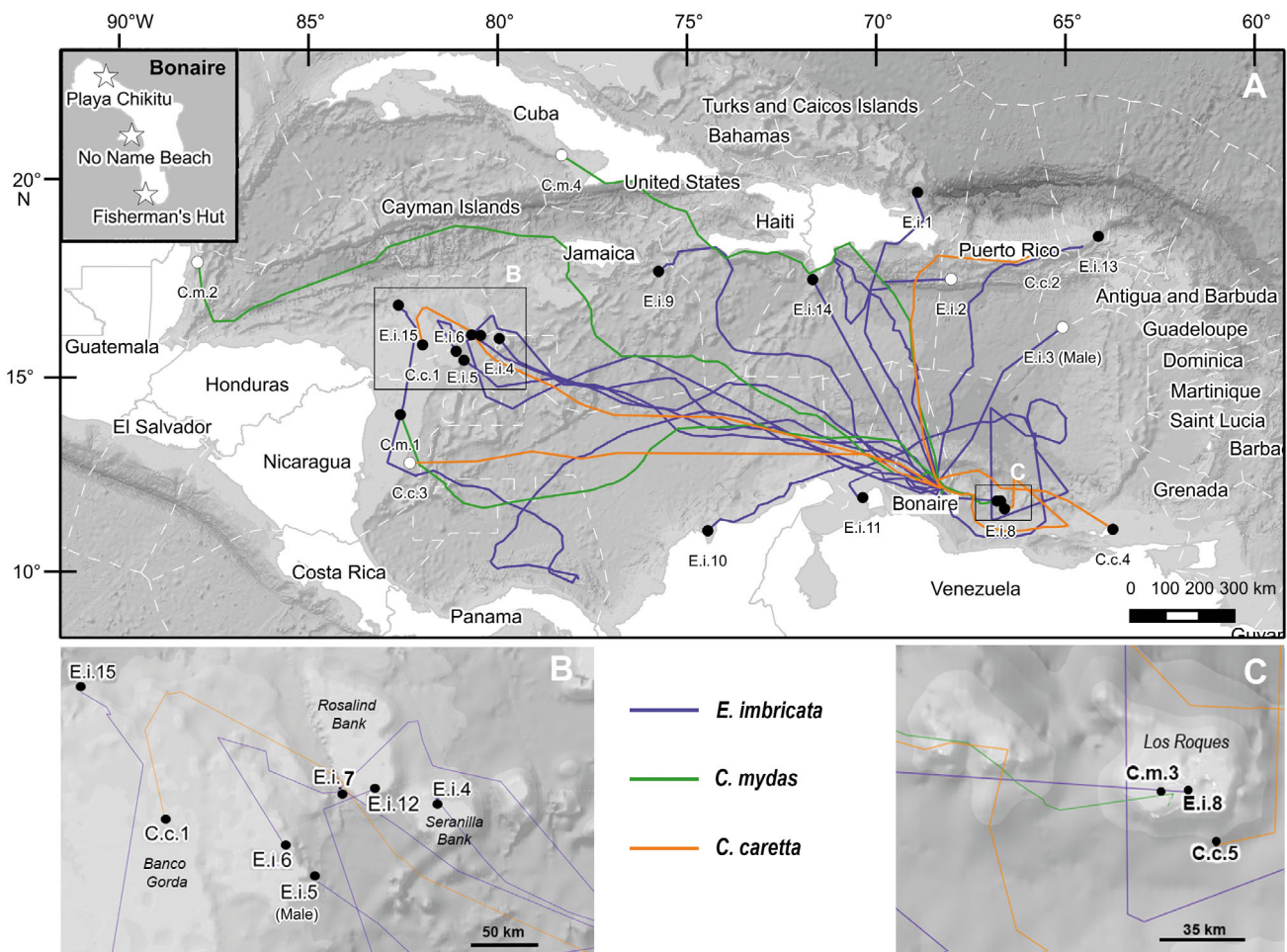


Fig. 1. Post-breeding tracks and foraging locations (black dots at end of tracks) for 5 loggerhead turtles (*Caretta caretta*; C.c.), 4 green turtles (*Chelonia mydas*; C.m.), and 15 hawksbill turtles (*Eretmochelys imbricata*; E.i.) from Bonaire and Klein Bonaire, Caribbean Netherlands. All tracked turtles were female, except 2 male hawksbill turtles 'male', see Table 1. White dots indicate last known location for turtles not tracked to their foraging grounds due to transmitter failure or loss. White dashed lines represent EEZ (exclusive economic zone) boundaries. (A) Post-breeding tracks across the Caribbean (inset upper left: capture locations on Bonaire & Klein Bonaire); (B) detail of Rosalind Bank, Serranilla Bank, and Banco Gorda; and (C) detail of Los Roques, Venezuela. Straight lines were drawn between reliable Argos locations, which resulted in migration lines crossing land for turtle C.m.4 and E.i.1.

versed the waters of 19 countries. Transmissions ceased for 5 turtles (CC3, CM1, CM2, CM4, EI3) 20, 30, 49, 35, and 14 d, respectively, after departing Bonaire, due to unknown causes. These turtles had not yet reached foraging grounds, as they were in waters >100 m depth, i.e. beyond the foraging depth range.

### Loggerhead turtle tracking

Five female loggerhead turtles were fitted with transmitters and tracked, 4 of these from the breeding grounds at Klein Bonaire (CC1–CC4) and 1 from the nesting beach at Playa Chikitu on the northeast coast of Bonaire (CC5) (Fig. 1A). Turtles departed 1–27 d after transmitter application, and then took 14–27 d to reach their foraging grounds, swimming 608–1766 km (Table 1). Loggerheads were tracked to offshore banks near Honduras (CC1) and Nicaragua (CC3) and to areas close to the islands of Vieques, Puerto Rico (CC2), Margarita Island (CC4), and Los Roques Archipelago, Venezuela (CC5). A visual survey in September 2005 of the foraging habitat used by CC2 off the west coast of Vieques Island, Puerto Rico, showed that at 5–12 m depth mixed-composition seagrass beds (dominated by *Thalassia testudinum* and *Syringodium filiforme*) could be found interspersed with a variety of macroalgae and abundant queen conchs *Lobatus gigas*.

### Green turtle tracking

Four female green turtles were tracked from nesting beaches on Bonaire; 3 of these (CM1, CM3, and CM4) were from Playa Chikitu, and one (CM2) was from an unnamed beach along the southwest coast (Fig. 1, Table 1). Turtles departed 1–62 d after transmitter application, then took 6–49 d to reach their foraging grounds, swimming distances of 198–3135 km. Two green turtles departed Bonaire on a northwest course, reaching Nicaragua (CM1) and the waters between Belize and Mexico (CM2). CM2 returned to nest 4 times on the beaches at Bonaire after transmitter application. This turtle swam extensively during her interesting periods of 14–18 d, covering distances of 129–599 km. Transmitter signals were lost for CM2 while the turtle was still making directed migratory movements, indicating that she may not yet have reached a foraging ground at her last recorded location. CM3 departed Bonaire towards

the southeast, reaching her foraging grounds at the Los Roques Archipelago, Venezuela. CM4 arrived in Dominican Republic waters in 6 d, continuing west along the coast of Haiti, and arriving in the proximity of the archipelago Jardines de la Reina, Cuba, when transmission ceased.

### Hawksbill turtle tracking

Two male (EI3 and EI5) and 13 female hawksbill turtles (EI1, EI2, EI4, and EI6–EI15) were tracked from the breeding grounds of Klein Bonaire. Males EI3 and EI5 remained for 93 and 151 d, respectively, near (<3 km) their capture locations before departure. Signals for one of the males (EI3) were lost after 14 d while traversing deep waters in the NE Caribbean Sea, and before reaching his foraging grounds. This turtle was captured again the following year (2005) in the breeding area off Klein Bonaire, still carrying the transmitter but without an antenna. EI5 reached his foraging grounds between Banco Gorda and Serranilla Bank, an offshore area between Honduras and Jamaica, after swimming a distance of 1522 km.

Female hawksbill turtles departed 1–56 d after transmitter application, then took 10–120 d to reach their foraging grounds; swimming distances were 197–3135 km. Five female hawksbills (EI4, EI6, EI7, EI12, and EI15) were tracked to the vicinity of Serranilla and Rosalind Banks, and established themselves on foraging grounds within <150 km of each other (Fig. 1, Table 1). Female EI2 was tracked to waters between Mona and Monito Islands, Puerto Rico. We checked the foraging habitat at Monito Island at 15–40 m depth and found that this area consists of a hard-bottom seafloor interspersed with sand patches and limestone boulders, with a high abundance of the prey sponge *Geodia neptuni*. The other hawksbills headed to foraging grounds by the Dominican Republic (EI1 and EI14), the Virgin Islands (EI13), Jamaica (EI19), Colombia (EI10), and Venezuela (EI18). Two female hawksbills (EI11 and EI15) took a long time to reach their foraging site after nesting, 120 and 100 d, respectively, taking considerable detours, in comparison to the other hawksbills. EI11 departed Klein Bonaire towards the south, beginning in large loops north of Los Roques and Orchila Islands, Venezuela, before reaching her foraging grounds off the west side of the Paraguaná Peninsula, Venezuela. EI15 swam west and south towards Panamanian waters, making 2 loops before heading north to Banco Gorda in Panama.



Table 1. Deployment data and results of transmitters placed on loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and hawksbill turtles (*Eretmochelys imbricata*) at Bonaire and Klein Bonaire, Caribbean Netherlands. Release locations were at Bonaire (B) or Klein Bonaire (KB). Dist. from release location: straight line distance from release location; M: male; F: female

Turtle ID	Sex	SCL (cm)	Date released	Release location	Transmitter model (d)	Tracking duration	Pre-departure period (d)	Travel time	Foraging ground name	Foraging ground location (km)	Dist. from release location (km)	Actual travel
<b><i>C. caretta</i></b>												
CC1	F	98.7	9 Jul 2004	KB	ST-20	109	1	27	Banco Gorda, Honduras	15.7174° N, 82.0204° W	1536	1766
CC2	F	92.8	24 Jun 2005	KB	ST-20	119	4	23	Vieques Island, Puerto Rico	18.2000° N, 65.5170° W	732	1074
CC3	F	90.4	19 Jun 2008	KB	ST-20	40	20	20	Nicaragua <sup>b</sup>	12.7970° N, 82.4060° W	1537	1604
CC4	F	90.2 <sup>a</sup>	2 Aug 2008	KB	ST-20	103	27	14	Margarita Island, Venezuela	11.0080° N, 63.7657° W	509	608
CC5	F	91.5	1 Aug 2011	B	Spot5	22	0	22	Los Roques Archipelago, Venezuela	11.7570° N, 66.8670° W	176	800
<b><i>C. mydas</i></b>												
CM1	F	95.5	31 Oct 2004	B	ST-20	128	1	30	Miskito Cays, Nicaragua <sup>b</sup>	14.0352° N, 82.5463° W	1560	1880
CM2	F	94.5 <sup>a</sup>	25 Jul 2007	B	Spot4	112	62	49	Between Belize & Mexico <sup>b</sup>	18.8550° N, 87.6330° W	2202	2765
CM3	F	95.8 <sup>a</sup>	20 Sep 2010	B	Spot5	123	12	6	Los Roques Archipelago, Venezuela	11.8325° N, 66.8115° W	178	198
CM4	F	103	8 Oct 2012	B	Spot5	35	0	35	Jardines de la Reina, Cuba <sup>b</sup>	21.166° N, 78.754° W	1490	3135
<b><i>E. imbricata</i></b>												
EI1	F	88.2	24 Oct 2003	KB	ST-20	106	1	45	Navidad Bank, Dominican Republic	20.1380° N, 68.8290° W	886	1513
EI2	F	84.9	2 Nov 2003	KB	ST-20	114	41	21	Monito Island, Puerto Rico <sup>b</sup>	18.1250° N, 68.0035° W	662	924
EI3	M	85.2	13 Jul 2004	KB	ST-20	107	93	14	NE Caribbean <sup>b</sup>	16.3840° N, 64.8690° W	596	648
EI4	F	87.9 <sup>a</sup>	22 Nov 2004	KB	ST-20	103	16	34	Serranilla Bank, Honduras	16.0293° N, 79.9969° W	1335	1456
EI5	M	81.9	8 Jun 2005	KB	ST-20	206	151	24	Between Banco Gorda and Serranilla Bank, Honduras	15.4615° N, 81.0002° W	1423	1522
EI6	F	92.1	14 Oct 2005	KB	ST-20	62	6	48	Between Banco Gorda and Serranilla Bank, Honduras	15.4371° N, 81.0013° W	1422	1822
EI7	F	80	27 Oct 2005	KB	ST-20	72	16	46	Rosalind Bank, Honduras	15.9179° N, 81.1511° W	1451	1493
EI8	F	82.9	13 Jul 2006	KB	ST-20	210	23	10	Los Roques Archipelago, Venezuela	11.8294° N, 66.7072° W	175	197
EI9	F	84.9	13 Jul 2007	KB	ST-20	292	44	25	Albatross Bank, Jamaica	17.6954° N, 75.6325° W	1000	1376
EI10	F	81.9 <sup>a</sup>	1 Aug 2009	KB	ST-20	185	50	14	Near Isla Salamanca, Colombia	11.0853° N, 74.4775° W	686	799
EI11	F	83	16 Sep 2009	KB	ST-20	190	1	120	Paraguand Peninsula, Venezuela	11.9376° N, 70.3107° W	222	2683
EI12	F	83.0 <sup>a</sup>	3 Sep 2010	KB	Spot5	130	41	36	Rosalind Bank, Honduras	16.0625° N, 80.5133° W	1410	1669
EI13	F	91	7 Oct 2010	KB	Spot5	375	9	38	Anegada, British Virgin Islands	18.6015° N, 64.1602° W	870	964
EI14	F	80.2 <sup>a</sup>	14 Oct 2011	KB	Spot5	377	56	11	Jaragua, Dominican Republic	17.4500° N, 71.6390° W	691	1364
EI15	F	94.1 <sup>a</sup>	13 Sep 2013	KB	Spot5	104	0	100	Banco Gorda, Honduras	16.2556° N, 82.611° W	1620	3135

<sup>a</sup>Curved carapace length to straight carapace length (SCL) conversion using formulas in Teas (1993)

<sup>b</sup>Last known location for turtles not tracked to their foraging grounds due to transmitter failure or other cause

## DISCUSSION

Our results highlight the importance of the international (cross-boundary) conservation of marine turtles. In a 10 yr period, we tracked 24 marine turtles departing the breeding grounds at Bonaire and Klein Bonaire to visit neritic foraging grounds in 10 countries. These results have considerably expanded our knowledge of the geographic range of these small rookeries. The migratory paths observed in this study reveal the wide geographic range of all 3 marine turtle species breeding at Bonaire and Klein Bonaire, swimming 197–3135 km and crossing multiple jurisdictions. The long distances traversed by post-breeding turtles from small, isolated islands to foraging grounds have been documented in several other studies. For example, nesting hawksbill turtles in the Caribbean have been recorded to migrate 881 km from St. Eustatius (Esteban et al. 2015), 500 km from Barbados (Horrocks et al. 2001), 2051 km from Mona Island (van Dam et al. 2008), and 1666 km from the Dominican Republic (Hawkes et al. 2012). However, 2 female hawksbills (EI11 and EI15) displayed remarkable behavior by taking 3–10 times longer than the other hawksbills to reach their foraging site after nesting, i.e. 120 and 100 d. Their route took considerable detours, with various loops covering the most kilometers of all the tracked turtles in this study, making it appear more like ‘meandering’ than directed migration. Esteban et al. (2015) reported similar meandering behavior of a post-nesting female hawksbill turtle from St. Eustatius, where the turtle travelled 200 km westward before reversing direction and settling within 50 km of the original nesting beach. It is unclear what the cues may be for such extended migratory routes.

Some of the turtles from this study migrated north towards Haiti, the Dominican Republic, and Puerto Rico, each individual going to a different foraging ground. Half the turtles headed west, predominantly migrating to shallow areas between Jamaica, Nicaragua, and Honduras, crossing through the EEZ of at least 7 countries (Caribbean Netherlands, Venezuela, Colombia, Jamaica, Nicaragua, Panama, and Honduras). The tracks in this study suggest the presence of a possible migratory corridor between Bonaire heading north-west to foraging grounds in Nicaragua and Honduras. Although the turtles tracked in this study did not concentrate on a single foraging ground, there were 2 areas that were frequented by all species: Los Roques (Venezuela) and the continental shelf of eastern Honduras and northern Nicaragua (Fig. 1B). The offshore area of Honduras and

Nicaragua is comprised of extensive shallow-water banks composed of coral reefs and seagrass beds, including named complexes such as the Miskito Cays, Rosalind Bank, Serranilla Bank, and Banco Gorda (Table 1). This foraging area has also been reported to be frequented by adult loggerhead, green, and hawksbill turtles that have been tracked from nesting grounds in Puerto Rico, the Cayman Islands, Costa Rica, and the Dominican Republic (Blumenthal et al. 2006, Troëng et al. 2005a,b, van Dam et al. 2008, Hawkes et al. 2012). Clearly, this extensive and relatively remote foraging area off Nicaragua and Honduras is of critical importance for marine turtle populations throughout the Caribbean region.

Given the wide dispersal of adult marine turtles from Bonaire, there are many places throughout the Caribbean where marine turtles continue to be at risk of legal or illegal harvest, which impacts conservation efforts and threatens turtle populations far removed from those territories. A point of concern is that Rosalind and Serranilla sandbanks have been subject to a sovereignty dispute between a number of countries who claim the banks in their EEZ (e.g. Honduras, Jamaica, Nicaragua, USA, and Colombia), which complicates adequate conservation management. Fishermen from many countries may now access the area with Rosalind and Gorda Banks being important fishing areas for Honduras, Nicaragua, and Jamaica (Aiken & Kong 2000). Harvest or unintentional killing of marine turtles on Rosalind and Serranilla Banks could result in the reduction of nesting populations across multiple jurisdictions in the Caribbean. Furthermore, the turtles in this study migrated across waters that have legal fisheries or reported bycatch of marine turtles in standard fisheries, notably Panama, Nicaragua, Honduras, Haiti, Colombia, and the British Virgin Islands (Campbell 2014, Humber et al. 2014). For example, 3 turtles from the present study passed or stayed near the coast of Nicaragua, where there is an ongoing green turtle fishery which accounts for 22% of the annual global take of marine turtles, predominantly green turtles (Lagueux 1998, Humber et al. 2014, Lagueux et al. 2014). Not only green turtles, but also hawksbill and loggerhead turtles are caught in this fishery, as well as incidentally by other fisheries in Nicaragua, such as by lobster divers, shrimp trawls, and in net sets (Lagueux 1998, Lagueux et al. 2003, Lagueux & Campbell 2005, Bräutigam & Eckert 2006). Furthermore, illegal fishing for turtles also continues to be a major cause of mortality across the Caribbean, both in countries where legal

turtle harvesting exists and in those where it is illegal (Bräutigam & Eckert 2006). Countries of particular concern for turtles breeding at Bonaire with regard to high mortality from such intentional illegal takes are Panama, Trinidad, Cuba, the Dominican Republic, Venezuela, Haiti, and Nicaragua (Campbell 2014). Results from the present study further underscore the need to mitigate the ongoing impact that turtle fishery, illegal take, and bycatch in the Caribbean could have on marine turtle populations throughout the Caribbean region.

Adult male turtles represented a minority in this study, 2 out of 24 tracked turtles. Males are generally under-represented in marine turtle tracking studies (Godley et al. 2008), mainly because they do not come ashore and therefore are less accessible to researchers. The 2 male hawksbills tracked in this study migrated greater distances (596–1423 km) than any male hawksbill from Puerto Rico (van Dam et al. 2008). A key observation in the current study is that the pre-departure periods for the 2 male hawksbills were 3–5 mo, which is a much longer period than that measured for females and longer than any previous recording. Our results indicate that these animals may expend significant effort on breeding or they may wait, post-breeding, for environmental cues to arise before departing. Male hawksbills, as opposed to females, typically feed while on the breeding grounds (van Dam et al. 2008) and therefore probably face less nutritionally driven urgency to return to their foraging grounds. Other studies have also reported that Caribbean hawksbills exhibit a migratory dichotomy, whereby some turtles remain in coastal waters close to the nesting beach and others migrate internationally (Horrocks et al. 2001, Moncada et al. 2012). For example, using tracking and tagging data combined, Esteban et al. (2015) found that some of the green and hawksbill females that nest in St. Eustatius and St. Maarten are year-round residents. Our study shows an intermediate pattern, where males remain resident for a quarter to half a year and then migrate internationally. In addition, male EI3 was recaptured on the breeding grounds at Klein Bonaire the subsequent year, similar to the 1 yr re-migration pattern reported for male hawksbills in Puerto Rico (van Dam et al. 2008). Based on these first observations of male hawksbill turtles it is possible that males migrate more often between foraging and nesting grounds while females migrate every 2 to 3 yr rather than annually. Our results highlight the need for further in-depth investigation into male marine turtle behavior and migration patterns.

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#### LITERATURE CITED

- Aiken K, Kong GA (2000) The marine fisheries of Jamaica. Naga. The ICLARM Quarterly 23:29–35. [http://pubs.iclarm.net/Naga/na\\_2365.pdf](http://pubs.iclarm.net/Naga/na_2365.pdf)
- Argos (2013) Argos user's manual. Argos/CLS, Toulouse. [www.argos-system.org/manual/home.htm](http://www.argos-system.org/manual/home.htm)
- Balazs GH, Miya RK, Beavers SC (1996) Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath JA, Barnard DE, Musick JA, Bell BA (eds) Proc 15<sup>th</sup> Annu Symp Sea Turtle Biology and Conservation. NOAA Tech Memo NMFS-SEFSC-387:21–26
- Blumenthal JM, Solomon JL, Bell CD, Austin TJ and others (2006) Satellite tracking highlights the need for international cooperation in marine turtle management. *Endang Species Res* 2:51–61
- Bowen BW, Grant WS, Hillis-Starr Z, Shaver DJ, Bjorndal KA, Bolten AB, Bass AL (2007) Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Mol Ecol* 16:49–60
- Bräutigam A, Eckert KL (2006) Turning the tide: exploitation, trade and management of marine turtles in the Lesser Antilles, Central America, Colombia and Venezuela. TRAFFIC International, Cambridge
- Campbell CL (2014) Conservation status of hawksbill turtles in the wider Caribbean, western Atlantic and eastern Pacific Regions. IAC Secretariat Pro Tempore, Falls Church, VA
- Debrot AO, Esteban N, Le Scao R, Caballero A, Hoetjes PC (2005) New sea turtle nesting records for the Netherlands Antilles provide impetus to conservation action. *Caribb J Sci* 41:334–339
- Dow Piniak WE, Eckert KL (2011) Sea turtle nesting habitat in the Wider Caribbean Region. *Endang Species Res* 15: 129–141
- Esteban N, van Dam RP, Harrison E, Herrera A, Berkel J (2015) Green and hawksbill turtles in the Lesser Antilles demonstrate behavioural plasticity in inter-nesting behaviour and post-nesting migration. *Mar Biol* 162: 1153–1163
- Godley BJ, Blumenthal JM, Broderick AC, Coyne MC, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endang Species Res* 4:3–22

- Hamann M, Godfrey MH, Seminoff JA, Arthur K and others (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endang Species Res* 11:245–269
- Hawkes LA, Tomás J, Revuelta O, Leon YM and others (2012) Migratory patterns in hawksbill turtles described by satellite tracking. *Mar Ecol Prog Ser* 461:223–232
- Hays GC, Scott R (2013) Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Funct Ecol* 27:748–756
- Hays GC, Åkesson S, Godley BJ, Luschi P, Santadrian P (2001) The implications of location accuracy for the interpretation of satellite tracking data. *Anim Behav* 61:1035–1040
- Hays GC, Mortimer JA, Ierodiaconou D, Esteban N (2014) Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. *Conserv Biol* 28:1636–1644
- Horrocks JA, Vermeer LA, Krueger B, Coyne M, Schroeder BA, Balazs GH (2001) Migration routes and destination characteristics of post-nesting hawksbill turtles satellite-tracked from Barbados, West Indies. *Chelonian Conserv Biol* 4:107–114
- Humber F, Godley BJ, Broderick AC (2014) So excellent a fish: a global overview of legal marine turtle fisheries. *Divers Distrib* 20:579–590
- Lagueux CJ (1998) Marine turtle fishery of Caribbean Nicaragua: human use patterns and harvest trends. PhD dissertation, University of Florida, Gainesville, FL
- Lagueux CJ, Campbell CL (2005) Marine turtle nesting and conservation needs on the south-east coast of Nicaragua. *Oryx* 39:398–405
- Lagueux CJ, Campbell CL, McCoy WA (2003) Nesting and conservation of the hawksbill turtle, *Eretmochelys imbricata*, in the Pearl Cays, Nicaragua. *Chelonian Conserv Biol* 4:588–602
- Lagueux CJ, Campbell CL, Strindberg S (2014) Artisanal green turtle, *Chelonia mydas*, fishery of Caribbean Nicaragua. I. Catch rates and trends, 1991–2011. *PLoS One* 9:e94667
- Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F (1998) The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc R Soc B* 265:2279–2284
- Luschi P, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Hays GC (2001) Testing animal navigational abilities in the ocean: displacement experiments on sea turtles. *Behav Ecol Sociobiol* 50:528–534
- Moncada FG, Hawkes LA, Fish MR, Godley BJ and others (2012) Patterns of dispersal of hawksbill turtles from the Cuban shelf inform scale of conservation and management. *Biol Conserv* 148:191–199
- QGIS Development Team (2015) QGIS Geographic Information System. Open Source Geospatial Foundation. <http://qgis.osgeo.org> (accessed 10 Jan 2016)
- Seminoff JA, Zárate P, Coyne M, Foley DG, Parker D, Lyon BN, Dutton PH (2008) Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endang Species Res* 4:57–72. doi:10.3354/esr00066
- Stapleton S, Nava M, Willis S, Brabec B (2014) Sea turtle conservation Bonaire: 2014 Technical Report, Sea Turtle Conservation Bonaire, Bonaire
- Teas WG (1993) Species composition and size class distribution of marine turtle strandings on the Gulf of Mexico and southeast United States coasts, 1985–1991. NOAA Tech Memo NMFS-SEFSC-315:1–43
- Troëng S, Dutton PH, Evans D (2005a) Migration of hawksbill turtles *Eretmochelys imbricata* from Tortuguero, Costa Rica. *Ecography* 28:394–402
- Troëng S, Evans DR, Harrison E, Lagueux CJ (2005b) Migration of green turtles *Chelonia mydas* from Tortuguero, Costa Rica. *Mar Biol* 148:435–447
- Van Dam RP, Diez CE, Balazs GH, Colón Colón LA, McMillan WO, Schroeder B (2008) Sex-specific migration patterns of hawksbill turtles from Mona Island, Puerto Rico. *Endang Species Res* 4:85–94
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS One* 5:e15465

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