Paper:
Esteban, N., van Dam, R., 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. *Marine Biology*
http://dx.doi.org/10.1007/s00227-015-2656-2

Green and hawksbill turtles in the Lesser Antilles demonstrate behavioural plasticity in inter-nesting behaviour and post-nesting migration

Nicole Esteban[1]*, Robert P. van Dam[2], Emma Harrison[3], Arturo Herrera[4], Jessica Berkel[5]

Manuscript version accepted by Marine Biology on 23 March 2015

[1] Department of Biosciences, Swansea University, Singleton Park, Swansea SA2 8PP, UK
[2] Chelonia Inc, PO Box 9020708, San Juan, PR 00902, Puerto Rico
[3] Sea Turtle Conservancy, Apartado Postal 246-2050, San Pedro, Costa Rica
[4] Centre for Ecology and Conservation, College of Life & Environmental Sciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK
[5] Statia National Marine Park, STENAPA, Gallows Bay, St Eustatius, Dutch Caribbean

*Corresponding Author: Nicole Esteban, Department of Biosciences, Swansea University, Singleton Park, Swansea SA2 8PP, UK. E-mail: n.esteban@swansea.ac.uk. Tel: +44 1792 513005. Fax: +44 1792 295452.

Abstract

Satellite transmitters were deployed on three green turtles, *Chelonia mydas*, and two hawksbill turtles, *Eretmochelys imbricata*, nesting in the Lesser Antilles islands, Caribbean, between 2005-2007 to obtain preliminary information about the inter-nesting, migratory and foraging habitats in the region. Despite the extremely small dataset, both year-round residents and migrants were identified; specifically (1) two green turtles used local shallow coastal sites within 50 km of the nesting beach during all of their inter-nesting periods and then settled at these sites on completion of their breeding seasons, (2) one hawksbill turtle travelled 200 km westward before reversing direction and settling within 50 km of the original nesting beach and (3) one green and one hawksbill turtle initially nested at the proximate site, before permanently relocating to an alternative nesting site over 190 km distant. A lack of nesting beach fidelity was supported by flipper tag datasets for the region. Tagging datasets from 2002-2012 supported that some green and hawksbill individuals exhibit low fidelity to nesting beaches, whereas other females exhibited a high degree of fidelity (26 turtles tagged, 40.0km maximum distance recorded from original nesting beach). Individual turtles nesting on St Eustatius

and St Maarten appear to exhibit behavioural plasticity in their inter-nesting behaviour and post-nesting migration routes in the Eastern Caribbean. The tracking and tagging data combined indicate that some of the green and hawksbill females that nest in the Lesser Antilles Islands are year-round residents, while others may nest and forage at alternative sites. Thus, continued year-round protection of these islands and implementation of protection programmes in nearby islands could contribute towards safeguarding the green and hawksbill populations of the region.

Introduction

Top pelagic predators such as tuna, sharks, sea turtles and cetaceans are widely dispersed across expansive ranges and therefore documenting behaviour in the open ocean presents considerable difficulties (Block 2005). The consequent incomplete baseline data on population status, spatial patterns and habitat use and the need for international coordination of conservation actions are amongst the challenges faced in promoting the protection and recovery of endangered, migratory marine species (Piniak and Eckert 2011). Satellite tracking technology allows remote tracking of migratory movements of these top pelagic predators and there is now a sizeable literature documenting advances in biotelemetry of various animal species with extensive ranges, with results enabling informed management decisions by fisheries and Marine Protected Area (MPA) managers worldwide (Hays et al. 2014a; Nielsen et al. 2009). Furthermore, biotelemetry has been increasingly used to improve our knowledge of spatial use and migratory pathways between breeding and foraging sites (e.g. Pendoley et al. 2014; Schofield et al. 2013).

In recent decades, satellite tracking technology has been proven the most suitable method for tracking the open-sea migratory journey of sea turtles (Papi et al. 2000) and has been fundamental in verifying inter-nesting patterns and migration routes of turtle populations from nesting beaches to foraging grounds (Broderick et al. 2007; Georges et al. 2007; Hawkes et al. 2011, Hays et al. 2014b). The high cost of satellite technology and lack of funding for tracking units has led to small sample sizes (e.g. Cuevas et al. 2008, Horrocks et al. 2008) and, by 2007, over 130 studies published whilst at least 200 studies have not yet been published in the peer-reviewed literature (Godley et al. 2007). However, various studies have demonstrated that it is possible to enhance small sample sizes from satellite tracking by integration of different technologies (i.e. stranding, capture-recapture, genetics, stable isotopes, modelling): by using datasets available from long term flipper tag programmes (e.g.

Troëng et al. 2005) or integrating satellite telemetry with remotely sensed ocean data (Seminoff et al. 2008). For instance, a recent study demonstrated that satellite tracking of 75 turtles produced similar information about migratory distributions to tag-returns published for the Mediterranean (Schofield et al. 2013).

Nesting site fidelity, ie. the propensity of individual adult female turtles to make repeated nesting emergences within a restricted geographic range, has been widely documented in the literature, and an early example found high nesting site fidelity amongst green turtles, *Chelonia mydas*, in Ascension Island (Mortimer and Portier 1989). Information on fidelity during inter-nesting movements has long been derived from tag-recapture studies (e.g. Limpus et al. 1992). More recently, satellite telemetry studies confirmed nesting site fidelity by green turtles, *Chelonia mydas* (Broderick et al. 2007, Whiting et al. 2008), hawksbill turtles, *Eretmochelys imbricata* (Parker et al. 2009; Walcott et al. 2012), leatherback turtles, *Dermochelys coriacea* (Byrne et al. 2009, Eckert et al. 2006) and loggerhead turtles, *Caretta caretta* (Broderick et al. 2007; Marcovaldi et al. 2010; Tucker 2010).

The current study focussed on two turtle species that both nest, and are year-round resident, on St Eustatius and St Maarten in the Dutch Caribbean Lesser Antilles (Debrot et al. 2005): the endangered green turtle (as assessed by Seminoff 2004) and critically endangered hawksbill turtle (as assessed by Mortimer and Donnelly 2008), with nesting by the latter species considered rare on these islands (Meylan 1999). On St Eustatius, flipper tagging of green and hawksbill turtles was conducted from 2002 during the main nesting season from early-July to late-September. No flipper tagging took place on St Maarten during the same period. Recapture of tagged individuals in this region has provided limited information on the turtles' migratory abilities, restricted to the date and location of the original tagging event and any subsequent recapture. Satellite telemetry allows us to address the question of inter-nesting area use and nesting site fidelity in more detail.

The aim of our study was to assess inter-nesting area use and nesting site fidelity in the Lesser Antilles. Based on our satellite tracking data for three green and two hawksbill turtles nesting on St Eustatius and St Maarten, combined with the flipper tagging dataset, we suggest strategies for (1) inter-nesting area use, (2) fidelity to nesting beaches and (3) migration strategies by adult female green and hawksbill turtles in the Lesser Antilles.

Methods

Study area and target species

The islands of St Eustatius (17.48°N, 62.97°W) and St Maarten (18.07°N, 63.05°W) are part of the Dutch Caribbean, which also includes the islands of Aruba, Bonaire, Curaçao and Saba. The islands are located in the Lesser Antilles in the North-eastern Caribbean (Figure 1), with land areas of just 21 km^2 and 52 km^2, respectively. Leatherback, green and hawksbill turtles nest on both islands. The study animals were female green and hawksbill turtles that emerged to nest in St Eustatius and in St Maarten.

The present study was conducted primarily in St Eustatius where a monitoring programme of nesting turtles by Statia National Marine Park has been in operation since 2002. Year-round, early morning surveys (0600-0800 hr) of the index beach took place according to a standard internationally recognised protocol for nesting beaches (Eckert et al. 1999). Any indication of turtle activity (i.e. tracks, sand disturbed in a way that is characteristic of nesting) was documented and the presence of eggs confirmed through careful digging by hand. Nightly beach patrols were conducted on Zeelandia Beach (1.0 km) and, when tidal conditions permitted, Turtle Beach (0.6 km). Hourly patrols were conducted by a minimum of two people between 2100-0400 hr. The primary objective of the beach patrols was to encounter as many nesting turtles as possible; to tag them with flipper tags, collect standard carapace measurements (curved carapace length notch to tip (CCL_{n-t}) and curved carapace width (CCW), mark the location of the nest for inclusion in a nest survivorship and hatching success study and relocate any nests laid in designated erosion zones. Tagging protocols detailed in Eckert and Beggs (2006) were used: all turtles were initially checked for tags and, if present, the numbers were recorded, as was the date, time and location. If no tags were present, the turtle was tagged with Inconel #681 metal flipper tags (http://www.nationalband.com). Tags were applied adjacent to the first large scale on the proximal part of the front flipper, where the swimming stroke will cause minimal tag movement (Balazs 1999). Tags were attached while the turtle was covering its nest immediately after laying eggs; so that the turtle was not disturbed prior to laying. Two metal tags were attached to each turtle; this was to ensure that even if one tag was lost the individual could still be recognised. Details of number, date, time and location of application of the tags were then recorded during patrols.

Satellite tag deployment

Nest monitoring results show that green and hawksbill turtles nest at St Eustatius during the months of April to November with a seasonal peak in nesting in September (STENAPA unpubl data). Satellite transmitters were deployed towards the end of the seasonal peak to increase the probability of encountering females at the end of their nesting season, and thus being able to track complete post-nesting migrations. Immediately after egg laying (or attempted egg laying) and once turtles were returning to the water, they were intercepted on the nesting beach and detained in a plywood box for transmitter attachment. Prior to attachment of the transmitter, the turtle carapace was thoroughly cleaned, which included removal of interfering external commensals such as barnacles. Transmitters of model ST-20 A-1010 (size, 12 x 6 x 3 cm; weight in air 280 g) (Telonics Inc, http://www.telonics.com) were applied to the highest point on the carapace using the silicone elastomer and fibreglass method of Balazs et al. (1996), modified by reinforcing the antenna base with a roll of fibreglass cloth placed on top of the transmitter immediately anterior to the antenna, as well as by placing hydrodynamically shaped filler material along the frontal area of the transmitter to streamline the package. Turtles were held for 1 to 2 h after attaching the transmitters to allow adhesives to set, then released at the location of capture.

Between September 2005 and September 2007, four female turtles (three green and one hawksbill) were fitted with satellite transmitters on Zeelandia Beach, St Eustatius. Additionally, one hawksbill was intercepted and equipped with a satellite transmitter on Guana Bay Beach, St Maarten. The attachment of all devices was conducted with permission from the Statia National Marine Park and St Maarten Marine Park.

Data analysis

The transmission durations from the two turtles tracked in 2005 lasted for much less time than expected according to the specifications of the transmitters (55 d and 69 d, pre-processed data) and remaining transmitters deployed in 2006 and 2007 were reprogrammed to improve the battery longevity and hence increase the amount of time that the transmitters would be able to send signals. Transmission durations from the three turtles tracked in 2006 and 2007 increased as a result of the re-programming (261 d, 146 d, 142 d, pre-processed data).

After attachment of satellite transmitters, locations were received from Service Argos and the online Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005) was used for managing the data. One copy of locations that had been uploaded twice was subsequently removed (Turtle B, *n* = 8). Studies by Argos (2013) and Hays et al. (2001) have shown that Argos location classes (LC) 3, 2, 1 and A are the most reliable, thus data in LC 0 and B (*n* = 1608) were removed prior to the plotting of tracks. Locations (*n* = 134) were filtered to exclude biologically unreasonable results for travel speed (>5kmh^{-1} (Luschi et al. 1998, 2001; Seminoff et al. 2008)). Data were further filtered (*n* = 533) to select the best location received on that day (defined as highest quality location class received that day; where two or more high-quality locations were received, we only used the first received that day). Filtering of the Argos-transmitted data resulted in the removal of 2283 locations in total (from *n* = 2479). A small number of locations (*n* = 14) were removed because they were visibly erroneous i.e. they were on land. As the 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.

For each turtle, total distance covered was computed by adding the distances between successive valid fixes. The straightness index was calculated as the ratio between the beeline distance from nesting beach to the last fix of a turtle's route and the total length of the route (Batschelet 1981). Evidence for subsequent nesting events on a different beach that was not patrolled was implied by locations close to potential nesting beaches corresponding with the expected inter-nesting interval for the species (12-16 d) (Hays et al. 2002).

Along with direct observation, when turtles were encountered nesting by a patrol in some cases, we used tracking data to infer whether turtles re-nested after satellite transmitter attachment and further categorise tracks as either inter-nesting or post-nesting tracks. Foraging sites were identified by visual assessment of mapped data and by individuals slowing down and remaining in fixed areas for extended periods of time of at least 3 weeks or until transmissions ceased (21-217 d).

Results

During patrols conducted between 2002 and 2012, 23 green turtles and three hawksbill turtles were flipper tagged when encountered while nesting on the index beach of Zeelandia Beach, St Eustatius. There were turtles nesting during this period that were not tagged due to logistical reasons. Reports from the morning track surveys for this 11 year period record the number of nests (probable and confirmed) as 255 (greens) and 104 (hawksbills) out of a total of 468 green- and 152 hawksbill nesting activities (JB, EH, AH, NE, STENAPA unpubl data). It is difficult to calculate an Estimated Clutch Frequency (ECF) and rookery population based on these low numbers of tagged turtles. Using calculated ECF from other Caribbean rookeries (greens = 3.0 in Florida (Johnson and Ehrhart 1996); hawksbills = 4.1 in Barbados (Beggs et al. 2007)), these results suggest a rookery population of 8 green turtles and two hawksbill turtles. This rookery size estimate is based on the assumption that nest counts are accurate as it is logistically challenging to dig up and verify that eggs have been laid for each track recorded as a nest. Hence, this crucial assumption has not been tested. These data are partially supported by a published record for turtles nesting in the Dutch Caribbean for the years 2002-4 (Debrot et al. 2005) and it was estimated that the number of flipper tagged turtles during 2002-2012 represented 26% and 14% of the green and hawksbill rookery populations respectively (STENAPA unpub data).

The five tracked turtles travelled from the nesting areas of St Eustatius and St Maarten to residence sites between 16 and 607 km straight-line distance away within three broad geographical areas in the Eastern and Central Caribbean (Figures 2 and 3). Tracking durations ranged from 31 to 237 d (mean ± SD = 120 ± 85 d, n = 5). A minimum duration of three weeks of tracking was considered sufficient to confirm that a turtle was resident and remaining in a fixed area. The mean number of Argos-relayed locations from these turtles was 0.40 d^{-1} (SD ± 0.19, range 0.09-0.61, n = 5). The size (CCL_{n-t}) of the five study animals was 113.5 cm, 112.0 cm, 106.0 cm (greens) and 85.5 cm, 82.0 cm (hawksbills).

Inter-nesting behaviour

Green turtles

Two turtles were observed nesting prior to satellite tag attachment (Turtle A on four occasions, Turtle C on one occasion). Subsequent to release, Turtle A was observed nesting on Zeelandia Beach 11 d after the previous observed nesting event. After attachment of the satellite transmitter, Turtle C remained in foraging grounds close to the coast of St Eustatius and headed to shallow waters of St Kitts (straight line distance 21.8 km). Positions close to a sandy beach indicated that it might nest but then showed a return to the primary nesting beach on St Eustatius and Turtle C was again observed returning to the sea from a false crawl, 11 d after nesting on Zeelandia (Table 2).

Prior to satellite transmitter attachment, one of the green turtles (E) had attempted to nest but was unsuccessful; and was intercepted on the way back to the sea. Turtle E then remained offshore around St Eustatius and satellite transmissions indicate a probable nesting event three nights later on Zeelandia Beach. Table 2 shows an observed inter-nesting interval (INI) of 11-12 d (Turtles A, C) for green turtles. Tag sighting records from 2002-2012 (JB, EH, AH, NE, STENAPA unpubl data) confirm that the green turtle individuals in the study exhibited typical INI for females of this species nesting on St Eustatius, varying from 9-13 d, supporting results from the satellite tracking (Turtles A, C). For example, the INI recorded for five clutches laid by Turtles A and E immediately prior to satellite tag attachment was INI = 11 and INI = 10-13, respectively. Tag sighting records from, St Kitts confirmed a green turtle tagged on St Eustatius nesting on North Friar's Bay beach, 40.0 km to the southeast (Stewart pers comm).

Hawksbill turtles

No inter-nesting behaviour was observed for Turtle B. Satellite tracking data from Turtle D indicate two probable nesting activities (Table 2). After satellite transmitter attachment, Turtle D immediately left St Eustatius, swimming north to St Barthélemy (straight line distance from release site of 48.7 km) and on to Scrub Island, North East of Anguilla (straight line distance from release site of 89.1 km) where Turtle D remained for several days, probably nested and then moved westwards towards deeper waters, changing southwards to St Croix, USVI, the site of another probable nest, a straight line distance of 203.2 km from the release site. Table 2 shows an inferred 16-17 d INI for this individual (Turtle D).

Migration and residence

Green turtles

Westward migration was shown by one turtle (E, Figure 2). Turtle E nested in St Eustatius in 2002, 2005, 2007, 2010 and 2012 indicative of a remigrant with regular migration patterns of 2-3 years. Immediately after the probable nesting event three days after satellite transmitter attachment took place, Turtle E headed north-westerly through the British Virgin Islands (BVI) (straight line distance of 203.1 km), past Puerto Rico (straight line distance of 355.7 km) to settle off El Macao, Dominican

Republic (606 km straight line distance in two weeks) . Transmissions ceased 116 d after arriving in foraging grounds.

No migration was shown by two turtles (A and C, Figure 3). Turtle A nested five confirmed times during the season and was then expected to migrate. All subsequent transmissions (42 d) showed her remaining within 5 km of the release site. Track surveys on St Eustatius showed that the last green turtle track of the season was 1 October 2005 and so it can be considered that Turtle A remained in foraging grounds around St Eustatius as uplinks record Turtle A was still in the offshore area >1 month after the 2005 nesting season had finished (last transmission was 2 November 2005). After attempted nesting on St Eustatius on 29 September 2006, Turtle C travelled around St Kitts to reach the shallow channel between St Kitts and Nevis, remaining until transmissions ceased after 237 d (straight line distance 47.3 km and total distance tracked 1061.7 km).

Hawksbill turtles

Both hawksbill turtles immediately departed from the nesting beach (B and D, Figure 2). Turtle B began a westward post-nesting migration from St Maarten and there was no evidence of subsequent nesting based on the tracking uplink data. This individual headed north-west toward Anegada (straight line distance of 155.1 km) swimming up to 60 km per day and then shifted her course abruptly to head to the south towards the Virgin Islands, travelling 289 km before reaching a foraging area close to Flanagan Island, BVI, 191 km straight-line distance from the release site, taking 10 d to reach the destination. Turtle B remained in the area until transmissions ceased after 57 d.

A circular pattern was shown by Turtle D and after the probable nesting activities on Scrub Island, Anguilla and St Croix, USVI, this individual completely changed direction and swam eastwards to return to Anguilla and St Maarten, settling in waters 20-35 m deep west of an uninhabited cay between St Barthélemy and St Maarten. This circular migration route of 880.6 km resulted in a final foraging site only 49.5 km straight line distance from the release site. Transmissions ended 104 d after arrival at the foraging location.

Discussion

The overriding conclusion of the current study is that individuals nesting on St Eustatius and St Maarten exhibit behavioural plasticity in their inter-nesting behaviour and post-nesting migration routes in the Eastern Caribbean. All turtles tracked during this three year study exhibited nesting behaviour patterns (INI, number of nests) similar to those previously reported for these two species in the Caribbean region; however some unusual post-nesting migration behaviour was observed and our data are not consistent with the generally accepted hypothesis that adult female greens and hawksbills in the Caribbean are migratory. Results demonstrate that green and hawksbill turtles in tropical areas exhibit different nesting and post-nesting strategies. Two nesting strategies were apparent in that some turtles repeatedly nest on the same beach, whilst others nest on beaches separated by over 190 km. Post-nesting strategies included migration to disparate foraging grounds as well as other turtles remaining at the nesting ground as year-round residents.

The green turtles showed use of an inter-nesting area of up to 21.8 km (including a foray to the neighbouring island of St Kitts) from the release site and indicated that nesting may occur on several islands in one season due to the close proximity of islands in this region of the Caribbean. This is supported by previous reports of St Eustatius tagged green turtles nesting on St Kitts (K. Stewart pers comm). While many populations of most sea turtle species exhibit general fidelity to nesting beaches, this study supports the few existing publications from the tropics showing that females may frequent a range of nesting beaches within an area of 25-200 km (e.g. Bjorndal and Bolten 2010). This lack of nesting site fidelity has been demonstrated for temperate regions and one key example is the observation of loggerhead turtles tagged on Zakynthos, Cephalonia or Kyparissia in the Mediterranean nesting at one of the other two sites. This movement has also been documented by satellite tracking studies, showing that females conducted "forays" of around 100 km to alternative sites (Cephalonia, Kyparrisia, Kotichi, Mesolonghi) from Zakynthos (Schofield et al. 2010). In the tropics, a key result of genetic analysis has been that loggerheads nested on several Cape Verde islands that were over 70 km distant and separated by waters over 1000 m deep (Marco et al. 2011). The size of this inter-nesting area is not surprising when compared to the reported inter-nesting area of green turtles within 135 km of the release site of Tortuguero, Costa Rica (Troëng et al. 2005). If an inter-nesting range of 135 km from a nesting beach is considered, then green turtles nesting on St Eustatius could be nesting internationally on at least nine other islands, including St Kitts, Nevis, Montserrat, Antigua, Barbuda, Saba, St Maarten, St Barthélemy and Anguilla.

A similar inter-nesting range is reported from Costa Rica (EH pers comm): every year a small number of green turtles (15-30) are encountered during night patrols in Tortuguero that have tags from monitoring and conservation projects run by other organisations at nesting beaches to the north and south along the Caribbean coast of Costa Rica. These beaches are anywhere from 1-100 km distance from Tortuguero National Park. In 2011, a green turtle was tagged on the nesting beach at Chiriquí Beach, Panama in June, and in September was encountered nesting at the southern end of Tortuguero National Park; a straight-line distance of approximately 260 km. At both locations the green turtle was believed to have nested successfully. These unpublished data, together with our results, further re-iterate the use of satellite tags to identify potential nesting sites for sea turtles. This approach was first implemented more than 20 years ago with studies of single loggerhead turtles (Hays et al. 1991) and has developed to studies of 30-60+ individuals (Kobayashi et al. 2011; Hawkes et al. 2011; Schofield et al. 2013; Pendoley et al. 2014).

The INI of hawksbills is generally longer than green turtles, for example mean ± SD = 14.9 ± 1.3 d reported from Barbados (Beggs *et al*. 2007) which supports the inferred nesting sites on Scrub Island, Anguilla (INI = 17) and St Croix, US Virgin Islands (USVI) (INI = 17) by Turtle D. Results for hawksbill turtles reflected reports from inter-nesting studies of hawksbill females tracked from beaches in St Croix, USVI which have suggested that females exhibit preferences for particular locations on the reef close to the primary beach (Starbird et al. 1999). This has been supported by studies of hawksbills nesting in Barbados (Welcott et al. 2012). The hawksbills in this study migrated to known hawksbill foraging grounds identified in previous studies (Boulon pers comm; RvD pers comm). This is also the case for a handful of hawksbill turtles encountered at Tortuguero in Costa Rica with tags from other nesting beach projects along the coast of Costa Rica (EH pers. comm.). The unusual pattern was the circuitous route shown by one hawksbill that travelled over 200 km to nest again and then returned to a foraging location less than 50 km from the original nesting site. This pattern has not been previously reported. However in other species there are occasional movements away from nesting areas before subsequent return within the same season (Schofield et al. 2010) and these movements may reflect prospecting searches for alternative nesting sites.

Turtles in this study showed a predominant westward movement which is similar to migration patterns from nesting grounds reported from several studies in the Eastern and Central Caribbean, including

Puerto Rico (van Dam et al. 2008); Cayman Islands (Blumenthal et al. 2006) and Dominican Republic (Hawkes et al. 2012). The Lesser Antilles separate the Caribbean from the Atlantic Ocean and act as a sieve for the inflow of Atlantic water to the Caribbean Basin, forming the Caribbean Current, the main surface circulation of the Caribbean Sea, consistent with observed and modelled patterns of ocean and wind-driven currents westward into the Caribbean through the Lesser Antilles passages north of Martinique at latitude ~15°N (Johns et al. 2002). The westward movement of the majority of turtles in this study and others cited supports the theory that adult migration is influenced by ocean current patterns experienced as hatchlings and small juvenile turtles (Hays et al. 2010b; Hays and Scott 2013; Luschi et al. 2003).

The non-direct routes to foraging sites have been discussed in previous studies whereby migrating turtles do not show a precise map sense and hence take non-optimum routes to their destination (Hays et al. 2014b). As with the individuals tracked in the current study, most turtles exhibit a correction in course during migration with multiple stages of travel to the vicinity of their final foraging destination. Typical course correction occurs along bathymetric contour lines around island groups, such as that shown by Turtle B travelling around small islands of the BVI, and then a binomial choice once the individual enters shallower waters of a larger island, as exhibited by Turtle E upon reaching the coastline of Dominican Republic.

Each of the green turtles settled in foraging grounds of relatively shallow (10-25 m) seagrass beds (St Eustatius, St Kitts, Dominican Republic) whilst the hawksbill turtles migrated to foraging grounds of mixed coral reef habitat (BVI, St Barthélemy). The island of St Barthélemy appears to be suitable foraging habitat for adult hawksbills, as another hawksbill was satellite tracked to the same area after nesting in 1998 at Mona Island, Puerto Rico (van Dam et al. 2008). Many of the foraging areas revealed by turtles' migration routes in this study have been previously documented (Revuelta et al. 2012; Debrot et al. 2005; Dow et al. 2007). Other foraging grounds have not been documented but are known locally, such as El Macao, Dominican Republic (Turtle E), an area of intense tourism development with nearby areas with less developed beaches and offshore seagrass habitat (Y. Leon pers comm) and the waters around Flanagan Island, BVI, a region with extensive reefs, algal plains and seagrass beds, suggesting there is adequate food close by (R. Boulon pers comm). Studies have 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;). This is not peculiar to the region; loggerheads in the Mediterranean and Atlantic exhibit alternative strategies such as coastal and oceanic foraging (e.g. Hawkes et al. 2012; Schofield et al. 2013). What is new is that the results from this study also suggest that Caribbean green turtles do not always migrate. Whilst this has been seen with green turtles in remote island systems such as Cocos Islands, Indian Ocean (Whiting et al. 2008), loggerhead turtles in Greece (e.g. Schofield et al. (2013) reported five of 75 tracked loggerheads remained resident at the breeding area), hawksbills in Cuba (Moncada et al. 2012) and in Hawaii (Parker et al. 2009), it is believed that this is the first documented case of Caribbean green turtles exhibiting non-migratory breeding and remaining within 50 km of the original nesting ground to forage. Clearly, if there are foraging resources at nesting sites, then a proportion of turtles may stay on site. With no resources being expended on migration, these green turtles might be able to reach reproductive condition more quickly and so show a reduced interval between successive nesting seasons. This has not been confirmed as there have been no observations of the two individuals at the nesting beach since the season in which they were fitted with satellite tags.

As with the majority of sea turtle tracking studies, only female nesting turtles were included in this study which involved a limited number of satellite transmitters (n = 5). It is important to increase the number of individuals satellite tracked to >40 (see Schofield et al. 2013) in order to draw further conclusions about population level dispersal of green and hawksbill turtles nesting on St Eustatius. There is also an urgent need to increase efforts to track male turtles to further understand the sex-specific patterns of migration between foraging and breeding habitats in the Caribbean. Significant differences have been observed in migratory range between males and females tagged in Puerto Rico (van Dam et al. 2008). Further afield, marked differences in male versus female breeding intervals have been revealed with males breeding more frequently than females in Australia (Limpus 1993) and Greece (Hays et al. 2010a). Increased understanding of patterns of behaviour of both sexes will ultimately be useful to provide data to improve and inform regional conservation policies.

The absence of migration in the female green turtles (with data still required about movements of male turtles) has implications for decisions about MPAs to simultaneously protect turtle nesting and foraging grounds in the Caribbean and other tropical areas. The presence of year-round resident females promotes the importance of year-round protection at key nesting sites, which would safeguard part of the two species' populations. Whilst much of the priority, to date, has been on the protection of nesting habitat, it may now be possible to identify areas using satellite tracking studies that incorporate foraging and nesting habitats and that, therefore, could provide improved protection for a sub-set of the turtle population in the region throughout their adult life. Information from satellite tracking studies in the Wider Caribbean, and further afield, can therefore allow researchers and conservation organisations to identify and rank critical habitat, inform policy-making, promote the implementation of regional agreements, and strengthen national and international conservation planning and research (e.g. Blumenthal et al. 2012).

In the Caribbean, examples for regional integration of research on turtles into nature policies and MPA management have been set by the DCNA and WIDECAST. Groups such as DCNA and WIDECAST are building biodiversity databases to collect data from individual organisations, such as conservation NGOs, and make data publically available. Improved communication and data sharing among everyone working on satellite tracking projects in the region will lead to a more coordinated approach to development of MPAs and turtle conservation/protection plans among all stakeholders. The current manuscript is the result of work by DCNA to promote understanding of sea turtles in the Dutch Caribbean, the data are freely available from the authors for further publications and it is hoped that increasing numbers of groups will make satellite tracking study data more publicly available for the benefit of international sea turtle conservation.

Results of this research, coupled with long-term monitoring of sea turtles nesting in St Eustatius, have enabled us to develop and communicate an understanding of management requirements for threatened green and hawksbill turtles in the Dutch Caribbean. This study highlights the value of international networking and data sharing, the benefits of collecting baseline information on the distribution and abundance of populations, and the usefulness of long-term, systematic monitoring of sea turtle nesting grounds: the tracking and tagging data combined indicate that some of the green and hawksbill turtles that nest in the Lesser Antilles Islands are year-round residents, while others may nest and forage at alternative sites. Thus, continued year-round protection of the Lesser Antilles Islands, and the expansion of protection measures to include islands within their potential inter-nesting range would contribute towards safeguarding the green and hawksbill populations of the region, to some extent.

Acknowledgements

NE, RvD and EH conceived the project and took part in fieldwork with assistance from AH and JB; NE led the analyses, interpretation of the data and writing with contributions from all authors. The authors wish to acknowledge use of the Maptool program (www.seaturtle.org) for analysis and graphics in this paper. Funding was provided by a grant from the Dutch Caribbean Nature Alliance (DCNA), additional funding and equipment was provided by WIDECAST and the Marine Turtle Tagging Centre in Barbados. The study was conducted within the Marine Park programmes and complied with all relevant national legislation. Numerous STENAPA and Nature Foundation St Maarten staff and volunteers are acknowledged for assisting in the attachment of satellite transmitters and monitoring activities between 2002-2012. We also thank the anonymous reviewers for their constructive suggestions to improve the manuscript.

References

Argos (2013) Argos User's Manual. Argos/CLS, Toulouse. http://www.argos-system.org/manual/home.htm. Accessed 13 December 2013

Balazs GH (1999) Factors to consider in the tagging of sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No 4, pp 101–109

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 (compilers) Proceedings of the fifteenth annual symposium on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-387, pp 21-26

Batschelet E (1981) Circular statistics in biology. New York: Academic Press

Beggs JA, Horrocks JA, Krueger BH (2007) Increase in hawksbill sea turtle *Eretmochelys imbricata* nesting in Barbados, West Indies. ESR 3(2):159-168. doi: 10.3354/esr003159

Block BA (2005) Physiological ecology in the 21st Century: Advancements in Biologging Science. Integr Comp Biol 45:305-320

Bjorndal KA and Bolten AB (2010) Hawksbill sea turtles in seagrass pastures: success in a peripheral habitat. Mar Biol 157:135-145

Blumenthal JM, Solomon JL, Bell CD, Austin TJ, Ebanks-Petrie G, Coyne MS, Broderick AC, Godley BJ (2006) Satellite tracking highlights the need for international cooperation in marine turtle management. ESR 2: 51-61

Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. Proc R Soc B 274: 1533-1538. doi: 10.1098/rspb.2007.0211

Byrne R, Fish J, Doyle TK, Houghton DR (2009) Tracking leatherback turtles (*Dermochelys coriacea*) during consecutive inter-nesting intervals: Further support for direct transmitter attachment. JEMBE 377: 68-75

Coyne MS, Godley BJ (2005) Satellite tracking and analysis tool (STAT): an integrated system for archiving, analysing and mapping animal tracking data. Mar Ecol Prog Ser 301:1-7

Cuevas E, Abreu-Grobois FA, Guzmán-Hernández V, Liceaga-Correa MA, van Dam RP (2008) Post-nesting migratory movements of hawksbill turtles *Eretmochelys imbricata* in waters adjacent to the Yucatan Peninsula, Mexico. ESR 10:123-133. doi: 10.3354/esr00128

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(2):334-339. ISSN: 0008-6452

Dow W, Eckert K, Palmer M, Kramer P (2007) An Atlas of Sea Turtle Nesting Habitat for the Wider Caribbean Region. WIDECAST and The Nature Conservancy. WIDECAST Tech Rep No. 6. Beaufort, North Carolina. 267 pp. ISSN: 1930-3025

Eckert KL, Beggs J (2006) Marine Turtle Tagging: A Manual of Recommended Practices, Revised Edition. WIDECAST Tech Rep No. 2. Beaufort, North Carolina. 40 pp. ISSN: 1930-3025

Eckert SA, Bagley D, Kubis S, Ehrhart L, Johnson C, Stewart K, DeFreese D (2006) Internesting and Postnesting movements and foraging habitats of Leatherback sea turtles (*Dermochelys coriacea*) nesting in Florida. Chelonian Conserv and Biol 5(2): 239-248

Georges JY, Billes A, Ferraroli S, Fossette S, Fretey J, Grémillet D, Le Maho Y, Myers AE, Tanaka H, Hays GC (2007) Meta-analysis of movements in Atlantic leatherback turtles during nesting season: conservation implications. Mar Ecol Prog Ser 338:225-232

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2007) Satellite tracking of sea turtles: Where have we been and where do we go next? ESR 3:1-20. doi: 10.3354/esr00060

Hawkes LA, Witt MJ, Broderick AC, Coker JW, Coyne MS, Dodd M, Frick MG, Godfrey MH, Griffin DB, Murphy SR, Murphy TM, Williams KL, Godley BJ (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Diversity Distrib 17:624-640. doi: 10.1111/j.1472.2011.00768.x

Hays GC, Webb PI, Hayes JP, Priede IG, French J (1991) Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. J Mar Biol Assoc UK 71:743-746

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, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD (2002) Water temperature and inter-nesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. J Thermal Biology 27, 429-432.

Hays GC, Fossette S, Katselidis KA, Schofield G, Gravenor MB (2010a) Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. Cons Biol 24:1636–1643. doi: 10.1111/j.1523-1739.2010.01531.x

Hays GC, Fossette S, Katselidis KA, Mariani P, Schofield G (2010b) Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. J R Soc Interface 7:1319-1327. doi: 10.1098/rsif.2010.0009

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. doi: 10.1111/1365-2435.12073

Hays GC, Mortimer JA, Ierodiaconou D, Esteban N (2014a) Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. Cons Biol 28:1636–1644. doi: 10.1111/cobi.12325

Hays GC, Christensen A, Fossette S, Schofield G, Talbot J, Mariani P (2014b) Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. Ecol Letters 17, 137–143. doi: 10.1111/ele.12219

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 and Biol 4(1):107-114

Johns WE, Townsend TL, Fratantoni DM, Wilson WD (2002) On the Atlantic inflow to the Caribbean Sea. Deep-Sea Res I 49:211-243

Johnson SA, Ehrhart LM (1996) Reproductive ecology of the Florida green turtle: clutch frequency. J Herp 30(3):407-410

Kobayashi DR, Cheng I-J, Parker DM, Polovina JJ, Kamezaki N, Balazs GH (2011) Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies. ICES J Mar Sci. doi:10.1093/icesjms/fsq185

Limpus CJ (1993) The green turtle, *Chelonia mydas* in Queensland: breeding males in the southern Great Barrier Reef. Wildl Res 20:513-523

Limpus CJ, Miller JD, Paramenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. Wildl Res 19(3):347-357

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: Biol Sci 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

Luschi P, Hays GC, Papi F (2003) A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103:293-302

Marco A, Abella Pérez E, Monzón Argüello C, Martins S, Araujo S, López Jurado LF (2011) The international importance of the archipelago of Cape Verde for marine turtles, in particular the loggerhead turtle *Caretta caretta.* Zoologia Caboverdiana 2(1):1-11. ISSN 2074-5737

Marcovaldi MÂ, Lopez GG, Soares L, Lima EHSM, Thomé JCA, Almeida AP (2010) Satellite-tracking of female loggerhead turtles highlights fidelity behaviour in northeastern Brazil. ESR 12:263-272

Meylan AB (1999) Status of the Hawksbill Turtle (*Eretmochelys imbricata*) in the Caribbean region. Chelonian Conserv Biol 3(2):177-184

Moncada FG, Hawkes LA, Fish MR, Godley BJ, Manolis SC, Medina Y, Nodarse G, Webb GJW (2012) Patterns of dispersal of hawksbill turtles from the Cuban shelf inform scale of conservation and management. Biol Cons 148:191-199

Mortimer JA, Portier KM (1989) Reproductive homing and inter-nesting behaviour of the Green Turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean. Copeia 4:962-977

Mortimer JA, Donnelly M (IUCN SSC Marine Turtle Specialist Group) (2008) *Eretmochelys imbricata*. The IUCN Red List of Threatened Species. Version 2014.2. www.iucnredlist.org. Downloaded on 05 October 2014

Papi F, Luschi P, Âkesson S, Capogrossi S, Hays GC (2000) Open-sea migration of magnetically disturbed sea turtles. J Exp Biol 203:3435-3443

Parker DM, Balazs GH, King CS, Katahira L, Gilmartin W (2009) Short-range movements of hawksbill turtles (*Eretmochelys imbricata*) from nesting to foraging areas within the Hawaiian Islands. Pacific Science 63(3):371-382. doi: 10.2984/049.063.0306

Pendoley KL, Schofield G, Whittock PA, Ierodiaconou D, Hays GC (2014) Protected species use of a coastal marine migratory corridor connecting marine protected areas. Mar Biol. doi: 10.1007/s00227-014-2433-7

Piniak WED, Eckert KL (2011) Sea turtle nesting habitat in the Wider Caribbean Region. ESR 15(2):129-141. doi: 10.3354/esr00375

Revuelta O, León YM, Feliz P, Godley BJ, Tomas J (2012) Protected areas host important remnants of marine turtle nesting stocks in the Dominican Republic. Oryx 46:348-358

Schofield G, Hobson VJ, Lilley MKS, Katselidis KA, Bishop CM, Brown P, Hays GC (2010). Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. Biol Conserv 143, 722-730. doi: 10.1016/j.biocon.2009.12.011

Schofield G, Dimadi A, Fossette S, Katselidis KA, Koutsoubas D, Lilley MKS, Luckman A, Pantis JD, Karagouni AD, Hays GC (2013) Satellite tracking large numbers of individuals to infer population level dispersal and core areas for protection. Divers and Distrib 1-11. doi: 10.1111/ddi.12077

Seminoff JA (Southwest Fisheries Science Center, US) (2004) *Chelonia mydas.* The IUCN Red List of Threatened Species. Version 2014.2. www.iucnredlist.org. Downloaded on 05 October 2014

Seminoff JA, Zárate P, Coyne M, Foley DG, Parker D, Lyon BN, Dutton PH (2008) Post-nesting migrations of Galápogos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. ESR 4: 57-72. doi: 10.3354/esr00066

Starbird CH, Hills-Starr Z, Harvey JT, Eckert SA (1999) Inter-nesting movements and behaviour of hawksbill turtles (*Eretmochelys imbricata*) around Buck Island Reef National Monument, St. Croix, US Virgin Islands. Chelonian Conserv Biol 3:237-243

Troëng S, Evans DR, Harrison E, Lagueux CJ (2005) Migration of green turtles *Chelonia mydas* from Tortuguero, Costa Rica. Mar Biol 148:435-447. doi: 10.1007/s00227-005-0076-4

Tucker AD (2010) Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock assessment. J Exp Mar Biol Ecol 383:48-55. doi: 10.1016/j.jembe.2009.11.009

van Dam RP, Diez CP, Balazs GH, Colon Colon LA, McMillan WO, Schroeder B (2008). Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico. ESR 4:85-94

Walcott J, Eckert S, Horrocks JA (2012) Tracking hawksbill sea turtles (*Eretmochelys imbricata*) during inter-nesting intervals around Barbados. Mar Biol 159:927-938. doi: 10.1007/s00227-011-1870-9

Whiting SD, Murray W, Macrae I, Thorn R, Chongkin M, Koch, AU (2008) Non-migratory breeding by isolated green sea turtles (*Chelonia mydas*) in the Indian Ocean: biological and conservation implications. Naturwissenschaften 95(4):355-60

Figures and Tables

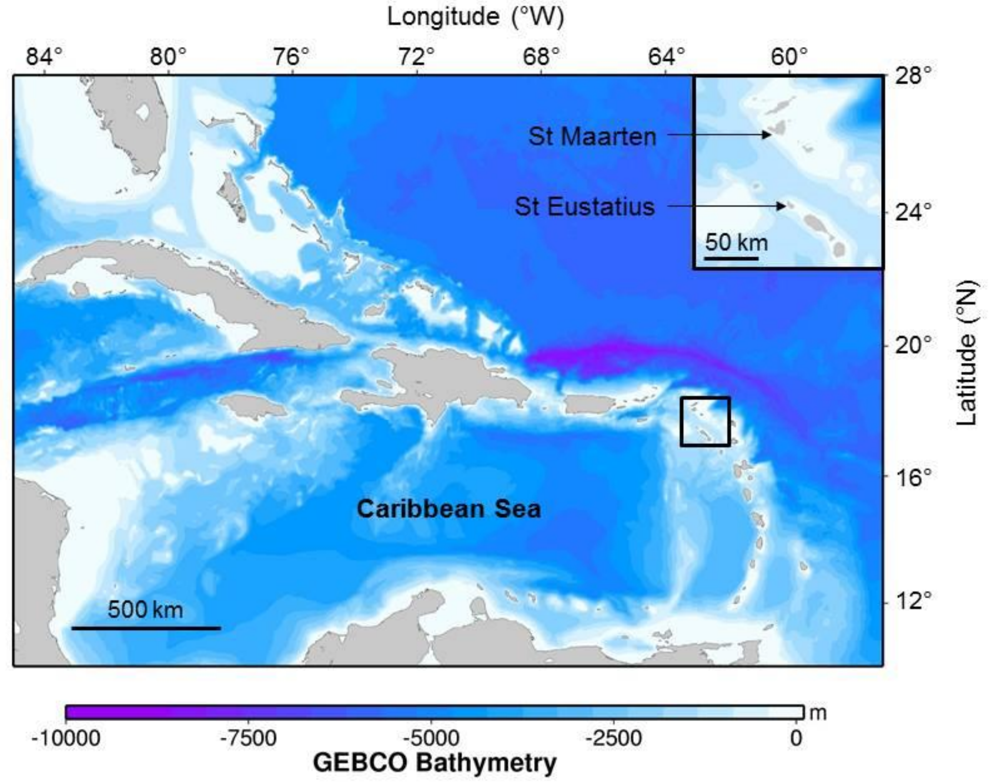

Figure 1 Location of study locations, the islands of St Eustatius and St Maarten in the Lesser Antilles (inset) in the North East of the Caribbean Sea.

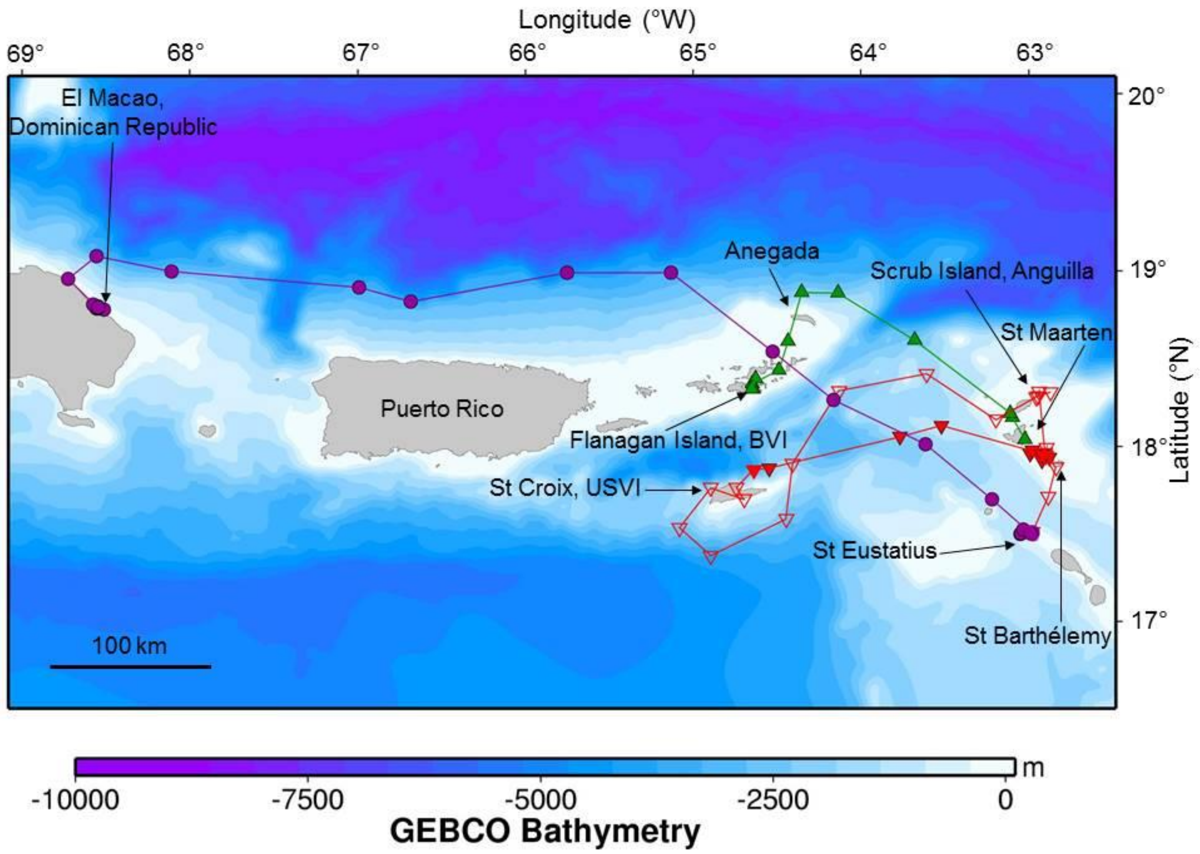

Figure 2 Migration patterns of three turtles subsequent to satellite transmitter attachment in St Eustatius and St Maarten, Dutch Caribbean, showing westward migration of one green (Turtle E – purple circles) and one hawksbill (Turtle B - green triangles) and circular migration of one hawksbill (Turtle D – red inverted triangles) returning to forage <50 km from the original nesting site. Points represent Class 1, 2, 3 or A quality points. Open symbols (Turtle D) represent points during inter-nesting periods, closed symbols are points indicating migration to foraging grounds.

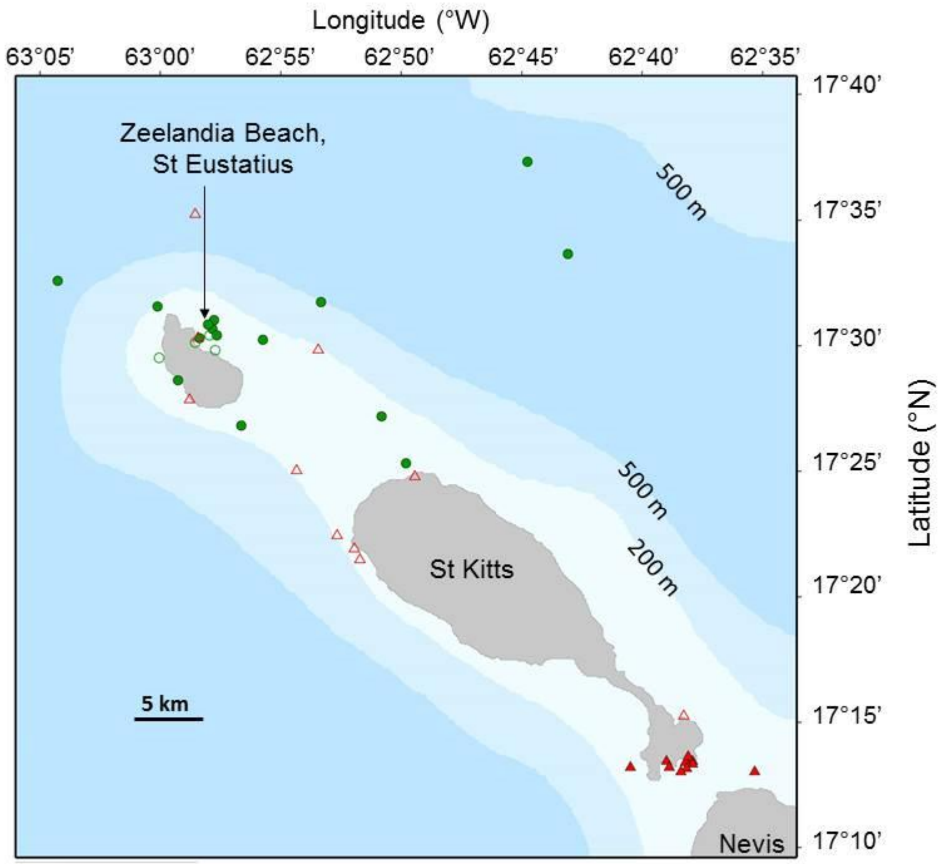

Figure 3 No or minimal migration shown by two green turtles (A and C), remaining in St Eustatius (Turtle A - green circles) and St Kitts & Nevis (Turtle C – red triangles) post-nesting. Points represent Class 1, 2, 3 or A quality points. Open symbols represent inter-nesting points or before settling at forage grounds, closed symbols are points at foraging grounds for 21 d. Results indicate that the area serves as a year-round foraging site as well as nesting ground.

Table 1 Details of the five turtles for which inter-nesting and post-nesting migrations were tracked by satellite for 31-26 data (CCL, curved carapace length tip to notch).

Turtle ID (Argos, Inconel)	Deployment location	Date transmitter deployed	Species	CCL (cm)	Deployment (inter-nesting) duration (d)	Foraging site (country)	Ma dis (k
A (60722, WE22/WE23)	St Eustatius	20/09/05	Green	113.5	42 (11)	St Eustatius	3
B (60726, N/A)	St Maarten	09/10/05	Hawksbill	82.0	31 (10)	BVI	2
C (60724, WE36/WE37)	St Eustatius	18/09/06	Green	106.0	237 (8)	St Kitts & Nevis	10
D (60725, WE34/WE35)	St Eustatius	08/09/06	Hawksbill	85.5	146 (10)	St Barthélemy	8
E (60723, WE24/WE25)	St Eustatius	02/09/07	Green	112.0	142 (26)	Dominican Republic	7

Table 2 Pre- and post-attachment nesting attempts for five turtles leaving St Eustatius and St Maarten. Confirmed nest were assessed by visual sightings (indicated by *). Inferred nesting attempts were assessed by comparison of ARGOS confirmed nesting attempts (INI, Inter Nesting Interval) using Argos data signal quality and frequency, and plots of dista

Turtle ID (Argos ref)	Nest years	Nests pre- (post-)	INI	Post-deployment nesting date	LC	Nesting location	Di (k
A (60722)	2005*	4 (+1)	11	01/10/05*	3	Zeelandia, St Eustatius	
B (60726)	2005*	1 (+0)	-	-	-	-	
C (60724)	2006*	1 (+1)	12	29/09/06*	2	Zeelandia, St Eustatius	
D (60725)	2006*	1 (+2)	16	25/09/06	3	Scrub Island, Anguilla	6
			33	12/10/06	2	NW St Croix, USVI	18
E (60723)	2002* 2005* 2007* 2010* 2012*	4 (+1)	3	04/09/07	-	-	