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Migration Routes and Destination Characteristics of Post-Nesting Hawksbill Turtles Satellite-Tracked from Barbados, West Indies

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Abstract. – Four post-nesting hawksbill turtles (*Eretmochelys imbricata*) in Barbados were fitted with satellite transmitters during the 1998 nesting season as part of a Caribbean-wide hawksbill research satellite tracking project to investigate whether adult females may undertake long-distance migrations between their nesting and foraging sites. The four study animals left Barbados waters immediately following their final nesting activity for the season and travelled for periods of between 7 and 18 days to reach foraging grounds in Dominica, Grenada, Trinidad, and Venezuela, respectively. Straight-line travel distances ranged from 200 to 435 km. All animals seemed to be influenced by water depth and geostrophic currents along their migration routes. The turtles generally travelled through shallower waters provided this did not result in travel against significant currents. In places where the turtles encountered currents moving in the desired direction of travel, their travel speeds increased markedly. Foraging home range sizes varied between 1.96–49.5 km^2 and were positively correlated with the average water depth, suggesting that turtles residing in deep water foraging areas may have to forage over larger areas to obtain sufficient food resources. All turtles settled at locations where sea conditions made them relatively inaccessible to fishermen, and this may be a key to their survival in countries where turtle fishing is permitted. The data indicate that adult females nesting in Barbados, where they are fully protected, may spend the majority of their lives in waters where they are only partially protected or unprotected.

Key Words. – Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; migration; foraging habitat; satellite telemetry; Barbados; Dominica; Grenada; Trinidad; Venezuela

The hawksbill turtle (*Eretmochelys imbricata*) is generally declining in the Caribbean, largely as a result of overharvesting (Meylan, 1999a), and is considered Critically Endangered by IUCN (Meylan and Donnelly, 1999). Juvenile and adult hawksbills forage in a wide variety of coral and sponge reefs, reef walls, and other hard-bottom habitats. They are primarily spongivorous (Meylan, 1988), and their role in regulating sponge growth on reefs may be significant (Hill, 1998). Hawksbill nesting seasons are generally at 2–3 year intervals, and they usually make 3–5 nests per season (see Crouse, 1999). Nesting is widely distributed throughout the Caribbean, but with the exception of Cuba and the Yucatan, Mexico (Carrillo et al., 1999; Moncada et al., 1999; Garduño-Andrade et al., 1999), the majority of countries record low numbers nesting. For example, in the Lesser Antilles, only 30–50 females are estimated to nest on each island annually (Meylan, 1999a).

Adult females have high reproductive value, and careful management of this component of the population is therefore particularly important in conservation. Since decreases in numbers of nesting females are the most visible index for population decline, many countries with declining nesting populations have already implemented partial or full protection measures. However, adult female hawksbills, which were once believed to be non-migratory (see Witzell, 1983), have recently been shown to migrate between breeding beaches, where they may spend only a few months every two to three years, and their foraging grounds where they spend most of their time (e.g., Miller et al., 1998; Meylan, 1999b; Hillis-Starr et al., 2000). Adult female hawksbills that are protected in countries where they nest may spend most of their lives in waters where they are either not protected at all or only partially protected. Information on where the females go once they leave the nesting beach, and the characteristics of their foraging habitats, is therefore important for successful conservation of the species.

Migration of hawksbills is poorly understood because conventional mark-recapture techniques often take years before a tag recovery is made. Even then, only the recapture location is known and not the migration route. With the exception of a small number of flipper tag returns (see Meylan, 1999b), little is known about the location of the feeding grounds of adult hawksbills in the Caribbean. However, recent advances in satellite telemetry offer the means to track sea turtles over long distances (Plotkin, 1998). To fix a location, the transmitter's antenna must break the water's surface for a sufficient time to allow several signals to be received by a satellite overhead. Satellite tracking of post-nesting hawksbills has to date been restricted to Mexico (Byles and Swimmer, 1994), the United States Virgin Islands (Groshens and Vaughan, 1993; Hillis-Starr et al., 2000), Hawaii (Balazs et al., 2000a) and the Seychelles (Mortimer and Balazs, 2000).

Barbados was one of six countries (also Antigua, USVI, Jamaica, Mexico, Puerto Rico) participating in a Caribbean hawksbill research satellite tracking project, a regional effort conceived and funded in part by the National Marine Fisheries Service, USA. The primary objective of the project was to identify where turtles nesting in each of six Caribbean territories spent their time between nesting seasons. In this paper, we report on the migration routes and environmental characteristics of the destinations of four adult female hawksbills fitted with satellite transmitters following nesting in Barbados, West Indies.

METHODS

Our subject animals were four adult female hawksbills ranging between 88–90 cm curved carapace length that were fitted with transmitters between 30 July and 1 August 1998. Following nesting, each female was briefly confined in a large open-topped wooden box, and transmitters were attached to the second vertebral scute of each animal using fiberglass following the basic procedures of Balazs et al. (2000a). The transmitters used were Model ST14 1.0 watt transmitters, custom built by Telonics, Inc., Mesa, Arizona, USA. Each measured 17 cm x 10 cm x 3.5 cm high and weighed 765 g. A 13 cm vertical antenna emerged from one end on the dorsal surface of the transmitter. The transmitter was placed on the turtle with the antenna at the posterior end. A piece of rolled fiberglass cloth soaked in resin was placed just anterior to the antenna base to reduce the likelihood of antenna abrasion and breakage at the point where it connects with the transmitter body. Two external electrodes (metal screws) acted as a saltwater switch which terminated transmissions and initiated collections of dive count data when immersed in seawater.

A transmitter cycle of 9 hours on and 3 hours off was selected so that transmissions would be in synchrony with satellites passing over the region. Service Argos Inc. (Argos, 1984) processed the data and distributed the results daily via e-mail. These data included the transmitter identification code to enable identification of the four different females, the location of each turtle as prescribed by Argos accuracy estimates (location classes, LC), the number of dives in the preceding 12 hours and the duration of the last dive prior to transmission. Three location classes were used in the present study (LC3, within 150 m of true position; LC2, 150–350 m from true position; and LC1, 350–1000 m from true position). Other location classes (O, A, and B) that have no defined accuracy estimate by Argos, were occasionally used in plotting the migration route where they appeared to be meaningful. Information presented on foraging ground locations in this study utilized LC1, 2, or 3 only.

ArcView GIS was used to interpolate 500 m isobaths of the migration routes from NOAA's ETOP05 5-minute gridded elevation data. An average water depth occupied by each female at her foraging destination was calculated using all fixes of location classes 1–3 plotted on bathymetric maps. Geostrophic or surface current maps were obtained from the Colorado Center for Astrodynamic Research Global Near Real-Time Altimeter Data Velocity Viewer. Maps are produced every 3 days, based on the latest 10 days of sampling, from satellite altimeter data collected by the National Research Laboratory at the Stennis Space Center. Geostrophic currents for a mid-migration date for each turtle were used to investigate whether currents influenced migration routes. Although there could be some changes in current speeds over the course of a single female's migration from nesting to foraging site, there were no significant changes in current direction.

RESULTS

Migration Routes

Characterization of Migration Routes. — Turtle 8179 was fitted with a transmitter on 30 July on Sandy Lane beach (13°16'97"N, 59°63'62"W) on the west coast of Barbados. The female swam around the island after leaving the nesting beach and then headed in an easterly direction on 1 August for a distance of about 50 km, before heading in a northwesterly direction (Fig. 1). She reached her destination off the northeast coast of Dominica (15°37'23"N, 61°16'55"W)14 days later, having covered a total distance of about 521 km (straight-line distance 334 km).

Turtle 8180 was fitted with a transmitter on Hilton beach (13°07'36"N, 59°60'64"W) on the south coast of Barbados on 31 July. She was observed nesting on four additional occasions before she left Barbados on 29 September immediately following her fifth nest for the season. She travelled in a westerly direction towards the northern Grenadines, then south to arrive at her destination 7 days later off the northeast coast of the Grenada islands of Carriacou and Petit Martinique (12°29'28"N, 61°21'32"W) (Fig. 2). She travelled a total distance of about 251 km (straight-line distance 200 km).

Turtle 8207 was fitted with a transmitter on Heron Bay beach (13°19'05"N, 59°63'62"W) on the west coast of Barbados on 31 July. She is believed to have nested (but was not observed) on an additional two occasions before she left Barbados waters on 29 August. She swam southwest on a course passing between Tobago and Grenada, then in a southeasterly direction to reach her destination 10 days later off the northeast tip of Trinidad (10°50'53"N, 60°54'04"W), a total distance travelled of 464 km (Fig. 3) (straight-line distance 284 km).

Turtle 8208 was fitted with a transmitter on Hilton beach (13°07'36"N, 59°60'64"W) on 1 August and was

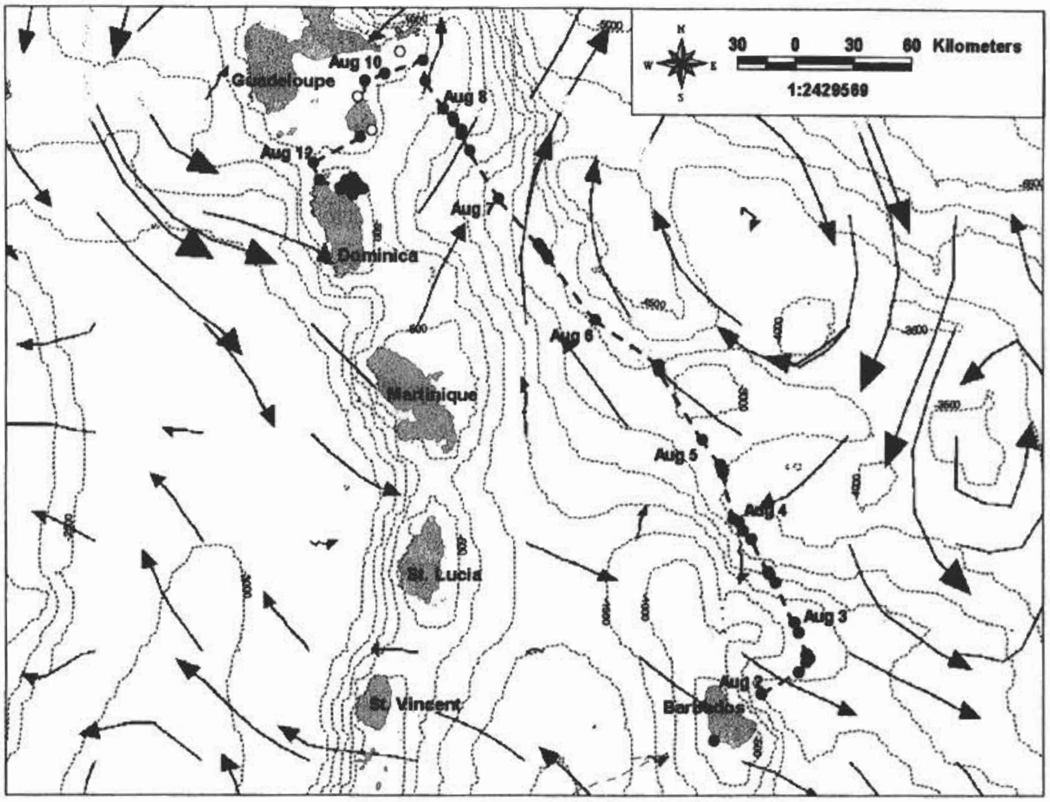

Figure 1. Post-nesting migration route (•—•—•) of hawksbill turtle 8179 between her nesting beach in Barbados and her foraging ground destination off Dominica (• location fixes of LC1–3; ○ location fixes LC < 1). Dates are provided for location fixes occurring at the same time of day on the date indicated. Geostrophic current directions are indicated by arrows, and strength of currents by the length of the arrow. Isobaths at 500 m intervals are indicated.

observed nesting on an additional two occasions before she left Barbados waters on 30 August. She swam in a westerly direction until she reached the Grenadine Islands, then headed south down the Grenadine Island chain before she swam in a west-southwesterly direction to her destination south of Venezuela's Los Testigos archipelago (11°11'20"N, 63°07'30"W) (Fig. 3). The first location fix received from this turtle on what presumably was her foraging ground was on 17 December, 18 days after she had left Barbados waters. Her route of 705 km was considerably longer than the 435 km which she would have covered if she had travelled directly between her nesting and foraging sites.

The four transmitters sent signals for 7.5–18 months. The first transmitter that stopped signalling (in May 1999) was on female 8208, who was resident in an area south of Los Testigos. Prior to complete cessation of signals from the transmitter, signals were received from an inland area on the Venezuelan island of Margarita. It is surmised that this female was captured and landed. The three other females remained in the same foraging locations, in each case for periods of 1–1.5 years, until transmitter batteries died.

Effects of Bathymetry and Geostrophic Currents on Migration Routes. — There appear to be no bathymetric features (e.g., areas of shallower water), that explain the initial easterly heading for 50 km taken by turtle 8179 (Fig. 1). However, current characteristics may have influenced her movement. At the time of year when she left Barbados waters, the strength of the northeast Trade Winds drops considerably, and prevailing northwest currents entering the eastern Caribbean tend to weaken. This may increase the significance of eddies that are created when the northwest flowing Atlantic water is forced over the shallow shelf of the island chain. As turtle 8179 left Barbados, the geostrophic currents she would have encountered to the north of Barbados would have been moving in a southeasterly direction. If she had immediately headed northwest from her west coast nesting beach, she would have been swimming against these currents for the entire distance to Dominica (see Fig. 1). Instead, she took a course that brought her into contact with a northwesterly moving current. When she encountered this current (between 4–5 August), her travel speed increased substantially. Currents moving in a northeasterly direction would have been encountered by the female as she passed to the northeast of Martinique. These may have caused her to overshoot Dominica (see Fig. 1). At this point, her speed slowed considerably and she took more than four days to travel the less than 100 km south-southwest to her destination off the northeast coast of Dominica.

Turtle 8180 travelled the most direct course of the four turtles. To avoid the deeper parts of the Tobago Trough, she would have had to significantly increase the length of her journey, but she crossed the deepest area (where water depths are greater than 3000 m) at its narrowest point (Fig. 2). She then entered the shallow waters of the Grenada Bank

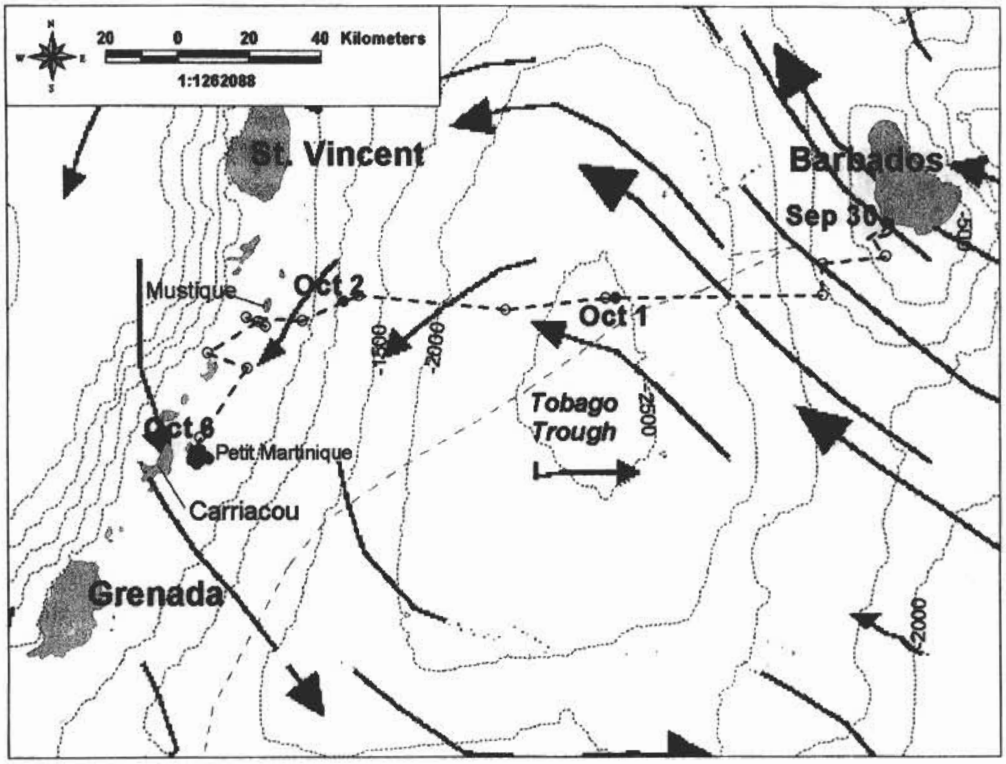

Figure 2. Post-nesting migration route (•—•—•) of hawksbill turtle 8180 between her nesting beach in Barbados and her foraging ground destination off Petite Martinique (Grenada) (• location fixes of LC1–3; ○ location fixes LC < 1). Dates are provided for location fixes occurring at the same time of day on the date indicated. Geostrophic current directions are indicated by arrows, and strength of currents by the length of the arrow. Isobaths at 500 m intervals are indicated.

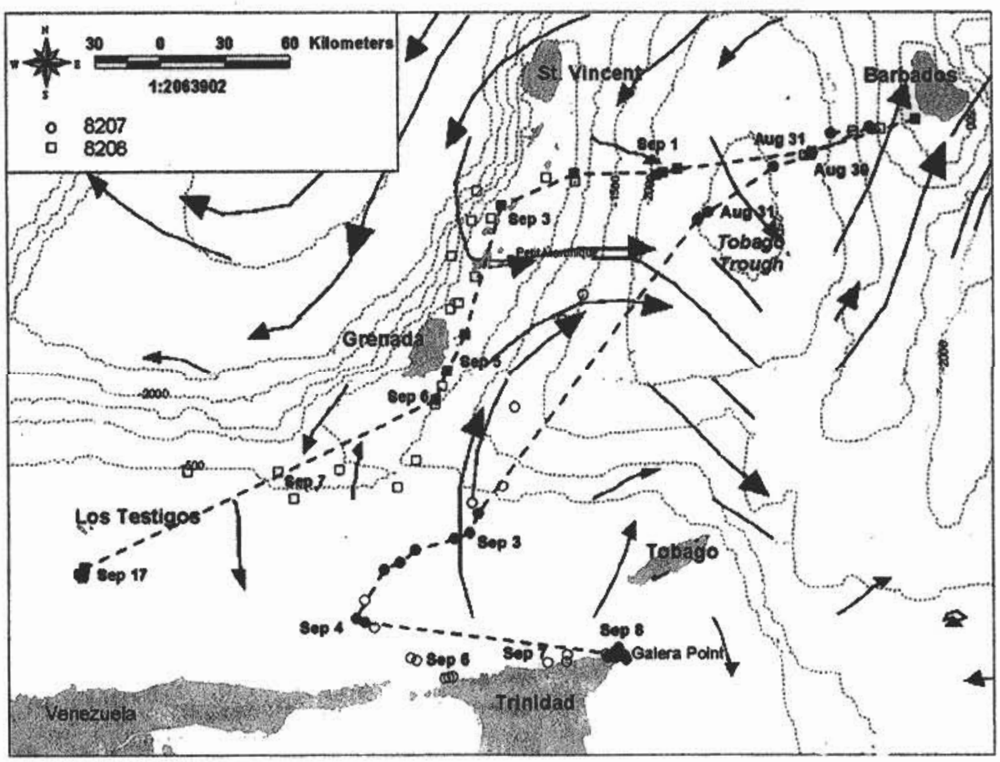

Figure 3. Post-nesting migration route of hawksbill turtle 8207 (•—•—•) between her nesting beach in Barbados and her foraging ground destination off Trinidad, and of hawksbill turtle 8208 (▪—▪—▪) between her nesting beach in Barbados and her foraging ground destination off Los Testigos (Venezuela) (• and ▪ indicate location fixes of LC1–3; ○ and □ indicate location fixes LC < 1). For each female, dates are provided for location fixes occurring at the same time of day on the date indicated. Geostrophic current directions are indicated by arrows, and strength of currents by the length of the arrow. Isobaths at 500 m intervals are indicated.

close to the northern Grenadine Island of Mustique, before travelling south to her destination east of Petite Martinique in the southern Grenadines (Fig. 2). Her travel speed dropped markedly as she travelled down the Grenadine Island chain, taking 4 days on this portion of her route before reaching her destination. Her slow travel speeds in the shallow waters of the island chain suggest that she may have fed periodically during this part of the journey.

Turtle 8207 left Barbados using a similar track as turtle 8180 as she entered the deep waters of the Tobago Trough. She appears to have crossed the deepest section via a longer route than turtle 8180, before moving into shallower water for the remainder of her journey. She could have remained in shallower waters for a greater part of the total distance between Barbados and Trinidad if she had travelled south from Barbados and passed to the southeast of Tobago. However, the geostrophic currents to the south of Barbados were moving strongly northeast (Fig. 3), which may have been a significant deterrent to her taking the more direct course over shallower waters. The route that she took enabled her to avoid strong counter-currents until she reached Grenada. At this point, strong northerly currents may have prevented her from taking a more direct course towards Trinidad. She was west of Trinidad before altering her course and approaching the island. Once in the nearshore waters of Trinidad, she benefitted from the easterly longshore current in reaching her destination.

Turtle 8208 (Fig. 3) travelled a similar course as 8180 (Fig. 2) and 8207 (Fig. 3) during the initial stages of her migration. She crossed the deepest portion of the Tobago Trough in the same location as turtle 8180, and then travelled down the Grenadine Islands chain in the shallow waters of the Grenada Bank. From there, she moved into the shallow waters of the South American continental shelf. She appeared to travel a course that minimized crossing waters deeper than 500 m, and indeed spent much of the time in waters considerably shallower than this. Her course carried her perpendicular to strong southeast and northeast currents for much of her journey.

The depth of water under each location fix (LC1, 2, or 3) was plotted against the average travel speed (mean km/day from fix location to next location at least 12 hrs apart) for all four turtles. There was a highly significant positive relationship between water depth and travel speed, with depth explaining 57% of the variation ($F = 42.3, p < 0.0001$). Travel speeds increased from an average of about 30 km/day in waters of less than 500 m depth to about 70 km/day in waters of 3000+ m depths.

Foraging Ground Characteristics

Turtle 8179 settled about 5 km off Crumpton Point on the northeast coast of Dominica (Fig. 4). The shelf of this volcanic island is at its widest at this point, but the bottom drops off quickly close to shore to more than 170 m. The three bays west of Crumpton Point have coral sand beaches, unlike other beaches in Dominica that are composed of weathered volcanic rocks. There is a coral reef system close to shore in this area, but the location data suggest that it was not used by 8179. Most of the location fixes placed 8179 in waters that are deeper than 50 m, with occasional forays into shallower waters of about 35 m depths and into waters deeper than 170 m. Daytime location fixes (between 0600–1800 hrs), i.e., times when she was most likely to be foraging, placed her in deeper water than nighttime location fixes (between 1800–0600 hrs) (Fig. 4). Her total home

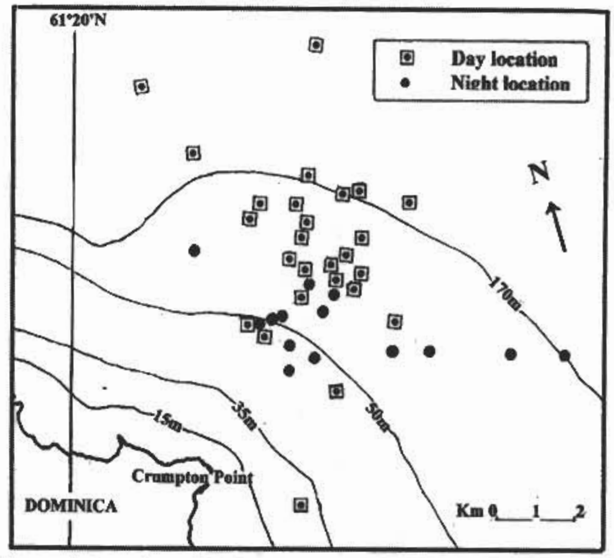

Figure 4. Location of the foraging ground of hawksbill turtle 8179 off the northeast coast of Dominica between 15 August 1998 and 1 February 2000. Location fixes of LC 1–3 during the daytime (0600–1800 hrs) and nighttime (1800–0600 hrs).

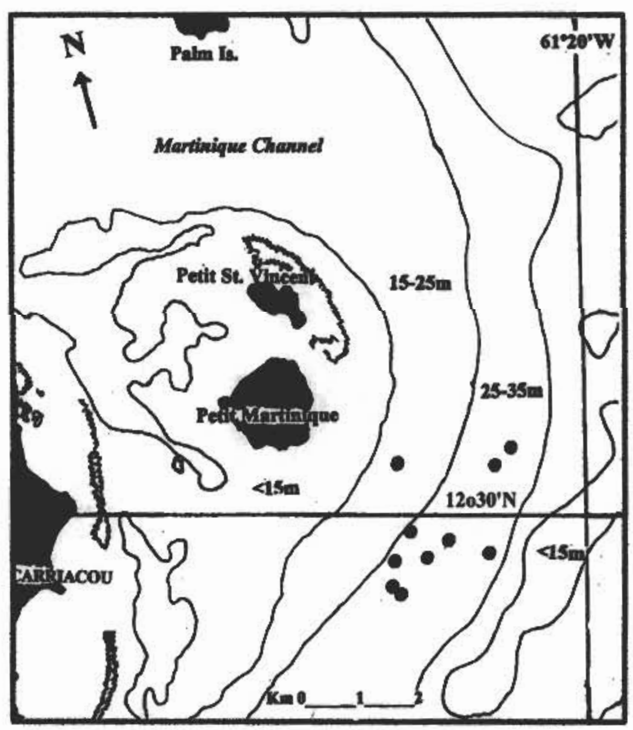

Figure 5. Location of the foraging ground of hawksbill turtle 8180 off the southeast coast of Petite Martinique (Grenada) between 6 October 1998 and 1 November 1999. Location fixes of LC 1–3 during the daytime (0600–1800 hrs).

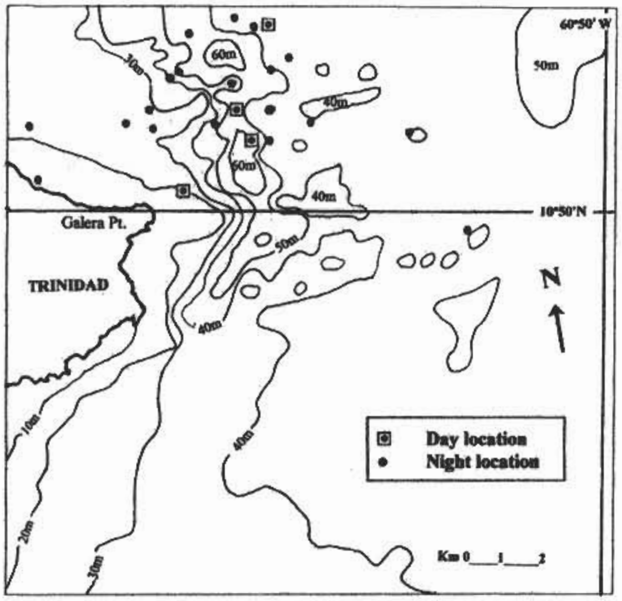

Figure 6. Location of the foraging ground of hawksbill turtle 8207 off the northeast coast of Trinidad between 8 September 1998 and 21 March 2000. Location fixes of LC 1–3 during the daytime (0600–1800 hrs) and nighttime (1800–0600 hrs).

range on the foraging ground was estimated to be 49.5 km^2 (Maximum Convex Polygon [MCP] Area).

Turtle 8180 was resident in an area of strong currents and choppy seas about 2.5 km southeast of Petit Martinique (Fig. 5). Most location fixes placed her in waters 25–35 m deep. All location fixes from this turtle occurred at night. This may suggest that she had been feeding in very shallow waters during the day. Since daytime surface intervals tend to decrease with decreasing water depth (van Dam and Diez, 1997), her surface intervals may have been insufficient for

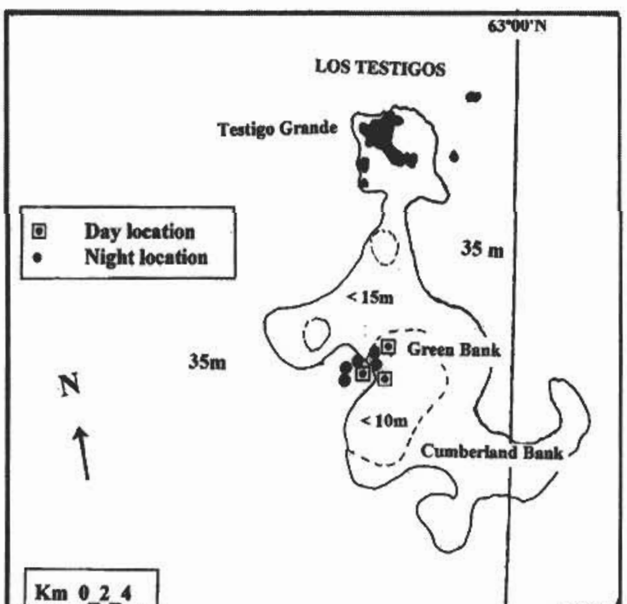

Figure 7. Location of the foraging ground of hawksbill turtle 8208 south of Los Testigos (Venezuela) between 17 September 1998 and 1 May 1999. Location fixes of LC 1–3 during the daytime (0600–1800 hrs) and nighttime (1800–0600 hrs).

daytime location fixes to be made. This turtle's home range on the foraging ground was estimated to be 11.27 km^2 (MCP).

Turtle 8207 settled off Galera Point on the northeast coast of Trinidad (Fig. 6). Nearby Toco Point is one of the only locations around Trinidad where local water conditions allow significant coral reef development, and hawksbills are regularly observed in this vicinity. However, most of the location fixes from 8207 placed her east of the reef area in turbid, choppy waters that are between 30–40 m deep. Her total home range on the foraging ground was estimated to be 24.6 km^2 (MCP). Here she may have been feeding on the sponges that are found in relative abundance in hard-bottom habitats on the east coast of Trinidad (S. Eckert, *pers. comm.*).

Turtle 8208 settled to the south of the Los Testigos archipelago (Fig. 7). Los Testigos are one third the distance between Margarita Island (Venezuela) and Grenada. She settled on the shallow (< 15 m deep) Cumberland Bank, which consists mostly of staghorn coral fragments, on the edge of the shallower Green Bank (< 10 m deep). The area is characterized by strong winds, currents, and turbulent waters, and is known for its abundance of lobsters, sardines, and sharks. Net and handline fishing is widespread. Juvenile turtles are also reported to be common. Fewer location fixes were recorded from 8208 than from the others, presumably because the shallow water resulted in surface intervals that were often too short to allow a fix to be made. The turtle's foraging range was calculated as 1.96 km^2 (MCP).

The four foraging grounds utilized by the turtles differed substantially in depth (range from < 10 m to > 50 m). Consistent with this, the four turtles differed significantly in average dive durations for both daytime dives (means ranging from 26–45 min, $F = 3.84$, $p = 0.01$) and nighttime dives (means ranging from 48–76 min, $F = 5.38$, $p < 0.01$). Daytime foraging dive durations in hawksbills, but not nighttime resting dive durations, have previously been shown to correlate with water depth (Van Dam and Diez, 1997).

DISCUSSION

The four adult female hawksbills fitted with transmitters in Barbados travelled for periods of between 7 and 18 days to reach their foraging grounds in Dominica, Grenada, Trinidad, and Venezuela. Our data are consistent with the hypothesis that adult female hawksbills in the Caribbean are migratory, and that they move through and are resident in the waters of several different Caribbean nations and territories during their lives. The distances between Barbados and the foraging grounds documented in this study ranged between 220 and 435 km, compared to 100–2000 km previously reported for other Caribbean hawksbills (Hillis-Starr et al., 2000), 135–315 km for Hawaiian hawksbills in the Pacific (Balazs et al., 2000a), up to 175 km for hawksbills in the Seychelles (Mortimer and Balazs, 2000) and 368–2425 km reported for northeast Australian hawksbills (Miller et al., 1998). Three of the four turtles remained resident in the foraging destinations for periods of over a year until the transmitter batteries died. The fourth was believed to have been captured either deliberately or incidentally after 7.5 months in residence at the Los Testigos foraging destination. Whether hawksbills occupy the same foraging areas between nesting seasons or whether they wander until they find suitable foraging habitat is an important issue that remains to be investigated.

All four females in this study appeared to be influenced by water depth and geostrophic currents along their migration routes. The data suggest that their preference may be to travel over shallow water masses when this does not result in being adversely affected by currents moving in undesirable directions. Moreover, when travelling over deeper water masses, they appear to swim faster than when travelling over shallower areas. Although turtles are clearly capable of swimming against currents during long-distance migrations (e.g., Balazs et al., 2000b; this study), making use of currents that are moving in the desired direction of travel is more energy efficient. In places where the turtles encountered currents moving in the desired direction of travel, their travel speeds increased markedly. Our data indicate that, for all females, the post-nesting migration began immediately following the last nesting activity. This suggests that the turtles do not feed in the proximity of their nesting sites before beginning their migration, and may feed little until they reach their foraging grounds. It may therefore be particularly important for post-nesting turtles with depleted fat reserves following months of breeding activity and little foraging to minimize the time and energy used to reach foraging grounds.

Foraging home range areas varied from 49.5 km^2 in Dominica to less than 2 km^2 in Venezuela. In all cases, the home ranges were substantially larger than home range sizes recorded for juvenile hawksbills at Mona Island, Puerto Rico (0.07–0.21 km^2, Van Dam and Diez, 1998), but were comparable to that reported for an adult female off Virgin Gorda in the British Virgin Islands (25 km^2, Hillis-Starr et al., 2000). Foraging home range sizes in the present study were positively correlated with the average water depth, suggesting that turtles residing in deep water foraging sites (e.g., 8179) may have to forage over larger areas to obtain sufficient food resources. As indicated by her longer average daytime dive duration (about 45 min), turtle 8179 undertook deeper foraging dives than the other three turtles (Fig. 8). Although foraging dives of 50–60 m are well within the reach of adult hawksbills, it is thought to be beyond their 'comfort zone' (R. Van Dam, *pers. comm.*). This again suggests that turtle 8179 was feeding in a suboptimal location. It is important to note that the small foraging home range recorded for 8208 in the shallow waters south of Los Testigos may in part have been attributable to the scarcity of location fixes from this turtle, caused by the short surface intervals between shallow foraging dives.

It is of interest that in all cases the females were resident in foraging grounds that were centered at least 2 km from shore, were often in deep water or in areas of strong currents, and often on the windward coasts of islands. Three of the locations (Dominica, Grenada, and Trinidad) still allow capture of hawksbills, but sea conditions at the foraging grounds at all three of these locations may make access by fishermen difficult. For example, although 8180 was in relatively shallow waters, there are strong currents in this area and turtle fishing is restricted to the leeward side of Carriacou or the leeward side of the barrier reef that protects the east coast of Carriacou. If hawksbills are faithful to specific foraging sites over many years, it is possible that these three females may have survived years of exploitation in the countries where they forage, only because they occupied sites that were relatively inaccessible to fishermen. In the one case where the female settled in shallow, accessible habitat (i.e., turtle 8208 near Los Testigos), the turtle was captured.

It is suggested by this study that the full legislative protection for hawksbills now provided in Barbados to facilitate population recovery will have limited effect if the females are spending most of their lives in the waters of countries that allow hawksbill fishing. Open season for turtle fishing in Dominica is 1 October and 19 February, for Grenada fishing for turtles is permitted between 1 September and 30 April, and in Trinidad fishing is allowed between 1 October and 28 February. Since the closed seasons are generally timed to encompass the peak hawksbill breeding season (i.e., June–October), the breeding populations in these countries are provided some degree of protection. However, the foraging populations that are resident year round in their waters, and which include breeding adults from other countries, are unprotected outside of the closed season. The information on post-nesting migratory behavior of Caribbean hawksbills provided in this study emphasizes the need for, at the very least, a regional integrated approach to protection of hawksbills in the Caribbean, if population recovery of this Critically Endangered species is to be realized.

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