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International Movements of Immature and Adult Hawksbill Turtles (*Eretmochelys imbricata*) in the Caribbean Region

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Abstract. – International movements of 19 adult and 9 immature hawksbills in the Caribbean region are summarized. Adult hawksbills traveled minimum distances of 110–1936 km, immatures traveled 46–900 km. These data and results of molecular genetic studies in the Caribbean refute the hypothesis that hawksbills are non-migratory. Compared with other marine turtle species, relatively few hawksbills have been tagged — an approximate cumulative total of 2500 individuals at the major nesting sites in the Caribbean during the last 40 years. International recapture rates of adult female hawksbills tagged on the nesting beach are on the order of 0–3.5%, which is comparable to those of other species of marine turtles that are considered to be highly migratory. High rates of local recapture of immatures on feeding grounds suggest long-term residency in developmental habitats. Knowledge of the schedules and routes of migrations is crucial to the effective management of hawksbills on both regional and multinational levels.

Key Words. – Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; migration; conservation; management; Caribbean

The proximity of suitable nesting beaches to coral reef feeding habitats in some parts of the tropics led early sea turtle researchers to speculate that hawksbill turtles (*Eretmochelys imbricata*), unlike the other species of sea turtles, did not need to undertake reproductive migrations (Carr, 1952; Bustard, 1979). This speculation was supported by the relatively small number of tagged females documented to be recaptured away from the nesting beach. Until recently, tag-and-recapture studies were nearly the only way in which researchers could study the migratory behavior of sea turtles. In the case of the hawksbill — whose populations are depleted worldwide — tag-return data have proven to be a poor indicator of migratory behavior because few tagging projects target this species and relatively few hawksbills have ever been tagged. For two decades, with limited evidence to the contrary, the hawksbill has been labeled as non-migratory, or even sedentary (Witzell, 1983).

With the accumulation of much additional research, scientists have gained a greater respect for the complex nature of sea turtle life histories and behavior. Tagging databases for some populations of sea turtles have grown quite large, and sophisticated technologies such as radio and satellite telemetry and molecular genetics have been incorporated into investigations of sea turtle ecology. In combination, these tools have led to many new insights into the long-distance movements of sea turtles, including a better understanding of migration.

A common finding of recent studies is that sea turtles do not always do what might be expected on the basis of logic and efficiency. Turtles have been shown to migrate thousands of kilometers to nest even when other suitable nesting beaches are closer. Limpus et al. (1992), for example, used data from tagging studies on the Great Barrier Reef, Australia, to show that loggerheads (*Caretta caretta*) foraging on Heron Reef within sight of the nesting beach on Heron Island migrated elsewhere to nest, whereas loggerheads from foraging grounds hundreds of kilometers away migrated to Heron Island to nest. Similar patterns have been reported in tagging studies conducted in other places and for other species, including the hawksbill (Nietschmann, 1981).

Bowen et al. (1996) used molecular data to show that the hawksbill population occupying the feeding grounds surrounding Mona Island, Puerto Rico — a regionally important nesting site — was not composed primarily of turtles that nest on Mona's beaches, but instead was largely composed of turtles from several distant rookeries. In the literature, there are relatively few examples of sea turtles nesting in the vicinity of their feeding grounds, although this certainly does occur (Nietschmann, 1981; Limpus, 1992; C. Diez, *pers. comm.*). Limpus et al. (1992) reviewed extensive tag return data for green turtles (*Chelonia mydas*) and loggerheads in Australia and concluded that, depending on the location of nesting beaches and feeding grounds used by individual turtles, the distances involved in migrations by these species in Australia might be long or short, representing a continuum. They considered there to be no "non-migratory" members of the populations, only some individuals that migrated very short distances.

For the hawksbill — a species considered "Critically Endangered" worldwide (Baillie and Groombridge, 1996; Meylan and Donnelly, 1999) and still highly sought-after for its valuable shell (tortoiseshell) — knowledge of its life-history stages and movements is extremely important for management purposes. A localized management strategy may only partially help to restore a population that is subject to mortality (including harvest) on a region-wide or international scale. Meylan (1982) reviewed published records of long-distance movements of hawksbills as documented by tag returns and concluded that there were insufficient data to base a conclusion about the migratory behavior of hawksbills. With the accumulation of an additional 17 years of data by various projects, a re-examination of the evidence is clearly warranted. The purpose of this paper is to review data from the Caribbean region, defined here in its broadest sense and referring to the area that encompasses the Caribbean Sea, Gulf of Mexico, and other tropical waters of the western Atlantic Ocean.

Despite great interest on the part of researchers, relatively few hawksbills in the Caribbean have been tagged. Widely dispersed nesting beaches, low nesting densities, and a long nesting season have thwarted concerted tagging efforts (Meylan, 1982). Since the late 1950s, when tagging of sea turtles became a routine practice, there have been few places in the Caribbean where tagging hawksbills has been productive enough to warrant the effort and funding. In recent years, the exception has been the Yucatán Península of Mexico, where there have been significant tagging efforts.

At many hawksbill nesting beaches, efforts are directed at counting or protecting nests, not at tagging nesting females. During most years, this is the case for many of the nesting beaches in Mexico, in Belize, and at Mona Island, Puerto Rico. Even where tagging is a priority, relatively few nesting females have been tagged: 328 at Tortuguero, Costa Rica, during the 44-year period from 1955 to 1998 (Caribbean Conservation Corporation, unpub. data); 123 at Jumby Bay, Antigua, from 1987 to 1996 (J. Richardson, *pers. comm.*); 105 at Buck Island Reef National Monument, St.

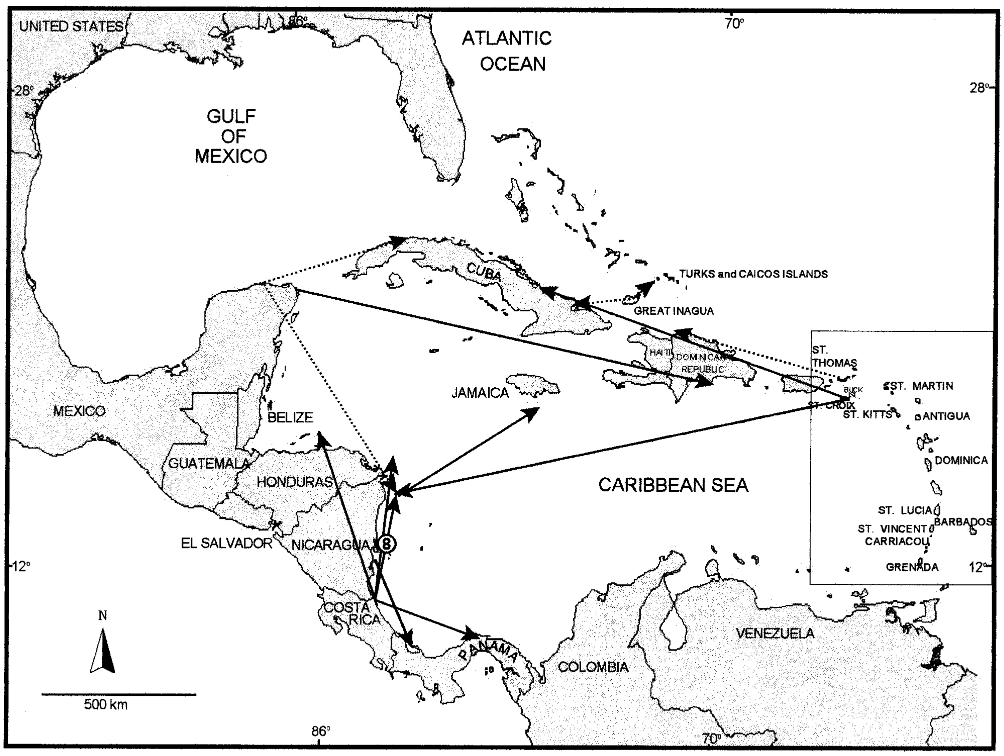

Figure 1. International movements of tagged hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean region. Arrows connect the tagging and recapture locations and do not imply travel routes. Solid lines represent adult turtles; dashed lines represent immatures. All arrows represent one animal except that connecting Tortuguero, Costa Rica, and Miskito Cays, Nicaragua (n = 8). See Table 1 for tagging and recapture dates, information on maturity status and sex, minimum distances traveled, and references.

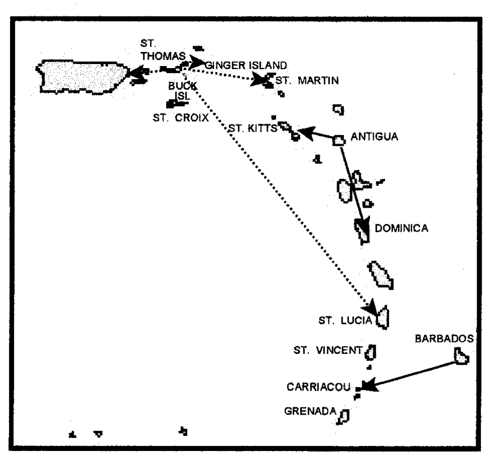

Table 1. International movements of wild hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean region, with dates tagged and recaptured. Km = minimum distance traveled in km, * = recaptured sometime before the recorded date.

Location Tagged	Sex	Tagged	Location Recaptured	Recaptured	Km	References
Adults						
Tortuguero, Costa Rica	female	8/18/56	Miskito coast, near Awastara, 24 km N Puerto Cabezas, Nicaragua	10/18/56*	385	Carr et al., 1966
Tortuguero, Costa Rica	female	7/27/59	Miskito Cays, Nicaragua	7/25/60	463	Carr et al., 1966
Tortuguero, Costa Rica	female	8/3/72	Miskito Cays, Nicaragua	11/73	385	Carr and Stancyk, 1975
Tortuguero, Costa Rica	female	8/26/72	Miskito Cays, Nicaragua	1/10/74	385	Carr and Stancyk, 1975
Tortuguero, Costa Rica	female	8/14/74	Miskito Cays, Nicaragua	12/8/77	385	Bjorndal et al., 1985; K. Bjorndal, *pers. comm.*
Tortuguero, Costa Rica	female	8/3/69	Miskito Cays, Nicaragua	5/70	385	Bjorndal et al., 1985; K. Bjorndal, *pers. comm.*
Tortuguero, Costa Rica	female	8/31/76	Rio Grande Bar, Nicaragua	5/24/83	385	Bjorndal et al., 1985; K. Bjorndal, *pers. comm.*
Tortuguero, Costa Rica	female	9/15/88	Tasbapune, Nicaragua	5/1/91*	200	Bjorndal et al., 1993; K. Bjorndal, *pers. comm.*
Tortuguero, Costa Rica	female	8/29/67	Colón, Panama	12/6/67	380	Bjorndal et al., 1985; K. Bjorndal, *pers. comm.*
Tortuguero, Costa Rica	female	7/23/77	Cay Gorda Bank, Honduras	5/15/79	541	Bjorndal et al., 1993; K. Bjorndal, *pers. comm.*
Tortuguero, Costa Rica	female	7/22/83	Isla Guanaja, Honduras	11/9/87*	850	Bjorndal et al., 1993; K. Bjorndal, *pers. comm.*
Sukra, Miskito Cays, Nicaragua	female	6/22/72	Pedro Cays, Jamaica	11/14/72	628	Nietschmann, 1981
Isla Mujeres, Yucatán, Mexico	female	7/6/67	Bani, Dominican Republic	4/25/71	1622	NMFS and USFWS, 1993; Márquez, 1990, 1996
Buck Island, St. Croix, USVI	female	7/9/90	Witties Cay, Miskito Cays, Nicaragua	1991	1936	Hillis, 1994; Z. Hillis, *pers. comm.*
Buck Island, St. Croix, USVI	female	7/28/97	Cayo Guajaba, Nuevitas, Cuba	2/9/98	1400	Z. Hillis, *pers. comm.*
Jumby Bay, Long Island, Antigua	female	6/18/91	Dominica	11/91	135	Fuller et al., 1992
Jumby Bay, Long Island, Antigua	female	8/6/87	Pelican Point, St. Kitts	—	110	J. Richardson, *pers. comm.*
Drill Hall, Barbados	female	7/8/96	Carriacou, Grenada	12/7/97	155	J. Horrocks, *pers. comm.*
Little Sandy Bay, Nicaragua	male	10/20/72	Almirante Bay, Panama	5/10/74	443	Nietschmann, 1981
Immatures						
Great Inagua, Bahamas	—	9/10/82	Providenciales, Turks and Caicos	9/26/83*	150	Bjorndal et al., 1985
Great Inagua, Bahamas	—	10/1/92	Banes, Cuba	8/97	200	Bjorndal and Bolten, 1998
St. Thomas, USVI	—	4/30/82	St. Lucia	8/1/83	650	Boulon, 1989
St. Thomas, USVI	—	1/28/82	Ginger Island, British Virgin Islands	6/15/85	46	Boulon, 1989
St. Thomas, USVI	—	10/29/81	East coast, Puerto Rico	5/87	95	Boulon, 1989
St. Thomas, USVI	—	6/21/83	St. Martin	6/87	185	Boulon, 1989
St. Thomas, USVI	—	12/7/84	Los Cayos de Monte Cristi, Dominican Republic	2/90	720	R. Boulon, *pers. comm.*
Las Coloradas, Yucatán, Mexico	—	7/91	Mariel, Cuba	7/94	560	M. Garduño, *pers. comm.*
Las Coloradas, Yucatán, Mexico	—	9/90	Miskito Cays, Nicaragua	3/96	900	M. Garduño, *pers. comm.*; C. Lagueux, *pers. comm.*

Croix, U.S. Virgin Islands, from 1988 to 1997 (Z. Hillis, *pers. comm.*); 978 in the state of Campeche, Mexico, from 1990 to 1998 (V. Guzmán, *pers. comm.*); 673 at Las Coloradas, Yucatán, Mexico, from 1985 to 1996 (Garduño and Márquez, 1994; M. Garduño, *pers. comm.*); 175 at Isla Holbox, Yucatán, Mexico, from 1988 to 1996 (J. Frazier, *pers. comm.*); and 121 at Mona Island, Puerto Rico, during 1974 and from 1984 to 1996 (Richardson, 1990; C. Diez, *pers. comm.*). These localities, at which a total of 2503 hawksbills have been tagged over approximately 40 years, represent the majority of sites in the Caribbean where hawksbills have been regularly tagged. Nesting females are the most accessible life-history stage for tagging, yet the number of hawksbill turtles cumulatively tagged on Caribbean nesting beaches over several decades is, at the maximum, a few thousand. In comparison, several thousand nesting green turtles may be tagged in a single year at a single beach, e.g., at Tortuguero, Costa Rica (Carr et al., 1978).

International movements of wild hawksbills tagged in the Caribbean region are depicted in Fig. 1 and listed in Table 1. The data in Table 1 are organized by maturity status and sex. Minimum distance traveled is calculated as the straight-line distance between tagging and capture sites via an at-sea route. Actual travel routes are likely not to be straight, and thus would involve greater distances.

Tag Returns of Adult Hawksbills

There were eleven international recaptures recorded of reproductive females tagged at the nesting beach at Tortuguero, Costa Rica. Eight of these occurred off the eastern coast of Nicaragua, two off Honduras, and one at Colón, Panama. Post-nesting movements of Tortuguero hawksbills show a pattern similar to that of Tortuguero green turtles (Bjorndal et al., 1985). Nietschmann (1981) tagged a total of 60 hawksbills in Nicaragua in 1972, including animals of both sexes and various size-classes up to reproductive adults. One adult female tagged on a reef in the Miskito Cays was taken on a nesting beach in Jamaica, a journey of at least 628 km. An adult male hawksbill tagged along the central part of the Nicaraguan coast was recovered 443 km away in Panama; this may be the only recorded migration of an adult male hawksbill. Nietschmann (1981) reported that both Cayman Brac (Cayman Islands, British West Indies) hawksbill fishermen and Miskitu Indian hawksbill fishermen in Nicaragua believed that hawksbills are migratory because of the turtles' seasonal disappearance and reappearance in particular areas. In Bocas del Toro, Panama, fishermen described the seasonal migration of hawksbills to Chiriquí Beach as having once been comparable to that of present day migrations of green turtles to Tortuguero, Costa Rica (A. Meylan and P. Meylan, unpubl. data).

The longest migrations documented for adult hawksbills in the Caribbean were of one adult female that traveled 1622 km, from the Yucatán Peninsula, Mexico, to the Dominican Republic, and of a second adult female that traveled 1936 km, from Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands, to the Miskito Cays, Nicaragua (Márquez, 1990; NMFS and USFWS, 1993; Hillis, 1994). The Caribbean records are comparable to the longest migrations of hawksbills observed in the Pacific — 2425 km for travel between Australia and Vanuatu and 2369 km for a journey from Australia to the Solomon Islands (Miller et al., 1998).

Two adult female hawksbills tagged while nesting at Jumby Bay, Antigua, were subsequently recaptured: one was recaptured 135 km away in Dominica, and the other was seen alive 110 km away in St. Kitts where its tag was read by a scuba diver (J. Richardson, *pers. comm.*).

There is also some evidence that hawksbills migrate between Guatemala and Belize — two hawksbills bearing tags with a Guatemalan return address were captured by fishermen in Belize (Smith, 1991; G. Smith, *pers. comm.*) — but detailed information is lacking.

For all the sea turtle species, the percentage of individual turtles that are tagged at a nesting beach and later captured in and reported from other countries is quite low (Meylan, 1982). The international recapture rate of green turtles tagged at Tortuguero, Costa Rica (8.9%) was among the highest observed among tagging projects reviewed by Meylan (1982). Solé (1994) reported a 1% international recapture rate for green turtles tagged at Aves Island, in the eastern Caribbean. The international recapture rate for loggerheads tagged at Melbourne Beach, Florida, from 1972 to 1978 was 0.3% (Meylan et al., 1983). The percentage of hawksbills tagged while nesting on Caribbean beaches and subsequently recaptured in other countries is as follows: 2% for Buck Island Reef National Monument, St. Croix; 1.6% for Jumby Bay, Antigua; and 3.5% for Tortuguero, Costa Rica. No international, post-nesting recaptures have been recorded for populations nesting at Mona Island, Puerto Rico, or Las Coloradas, Mexico. The percentages of hawksbill tag returns in the Caribbean that are international are thus within the range of those for other sea turtle species that are considered to be highly migratory.

Tag Returns of Immature Hawksbills

Table 1 and Fig. 1 also show international recaptures of immature hawksbills tagged on their feeding grounds (developmental habitats). Relatively few studies in the Caribbean involve tagging immature hawksbills, and the total number tagged is considerably less than that of nesting females. The high local recapture rates observed in several studies in the Caribbean (Nietschmann, 1981; Boulon, 1994; van Dam and Diez, 1998) indicate that immature hawksbills tend to remain in the same developmental habitats for extended periods. Limpus (1992) documented strong site fidelity among hawksbills tagged on their feeding grounds in Australia. Because of this tendency towards site fixity, one would not expect to see immature hawksbills move extensively unless they are relocating to other developmental habitats or from developmental habitats to adult feeding grounds.

Tag-return data from the Caribbean region support this theory. Of the 43 immature hawksbills that have been tagged at Magens Bay, St. Thomas, U.S. Virgin Islands, since 1981, 13 (30.2%) have been recaptured locally and 5 (11.6%) in other countries 46 to 720 km away (Boulon, 1989; R. Boulon, *pers. comm.*) (Table 1). Of 11 immature hawksbills tagged by Nietschmann (1981) in Nicaragua, 2 (18.2%) were recaptured locally, and none internationally. Of 57 immature hawksbills tagged in the waters of Buck Island Reef National Monument, St. Croix, since 1994, 18 (32%) were resighted locally, and none internationally (Phillips, 1996). Of 328 hawksbills tagged in the waters of Mona Island since 1992, 95 (29%) have been resighted locally, and none internationally (C. Diez, *pers. comm.*). Of 356 immature hawksbills tagged at Las Coloradas, Mexico, in 1990–95, 16 (4.5%) have been recaptured — 12 (3.4%) locally, 2 (0.6%) on the Campeche Banks, Mexico, and 2 (0.6%) internationally from 560 to 900 km away, in Cuba and Nicaragua (Garduño and Márquez, 1994; M. Garduño, *pers. comm.*; C. Lagueux, *pers. comm.*).

Of 604 hawksbills tagged at numerous sites in Cuban waters from 1989 to 1995, 46 (7.6%) were recaptured as of 1996, all in Cuban waters (Republic of Cuba, 1997). The distance traveled by recaptured turtles varied markedly. All of the 15 hawksbills tagged in the Doce Leguas area were recaptured locally (< 10 km); however, all of those tagged at Nuevitas and Las Tunas had traveled away from the tagging site, some as far as 744 km. Two immature hawksbills captured in Cuban waters were originally tagged in Yucatán, Mexico, and Great Inagua, Bahamas (Bjorndal and Bolten, 1998; M. Garduño, *pers. comm.*) (Fig. 1).

Movements of immature hawksbills can be extensive. A 74 cm wild subadult hawksbill tagged on feeding grounds at Atol das Rocas in Brazil was captured six months later at Dakar, Senegal, 3680 km away (Marcovaldi and Filippini, 1991). Whether this represents a migration or random dispersal remains unknown. Immature hawksbills initially reared in captivity (head-started) at Los Roques, Venezuela, have been recovered elsewhere in Venezuela, in Bonaire, Colombia (including San Andrés Island off Nicaragua), Jamaica, Bahamas, Belize, Honduras, Panama, the Dominican Republic, and Cuba (E. Weil, *pers. comm*.). Two hawksbills head-started in Yucatán, Mexico, were recaptured off the southern coast of Cuba (Márquez, 1990; R. Márquez, *pers. comm*.). Although the migratory behavior of head-started turtles most certainly can be expected to differ from that of wild turtles, these data demonstrate the capability of immature hawksbills to travel long distances.

Telemetry and Genetics Data

Knowledge of hawksbill movements can be expected to increase greatly with the application of satellite tracking technology. However, to date, hawksbill turtles have been the subject of only a few satellite tracking studies in the Caribbean. Early efforts by Groshens and Vaughan (1994) at Buck Island Reef National Monument in St. Croix, U.S. Virgin Islands, were hampered by equipment problems and produced limited data. Byles and Swimmer (1994) satellite-tracked four adult female hawksbills tagged in Campeche and Yucatán, Mexico; detailed results of these experiments have not yet been published. Satellite tracking experiments of hawksbill turtles have recently been initiated at several sites in the Caribbean.

In a satellite telemetry study of hawksbills in the Pacific, Balazs et al. (1996) observed mainly coastal, short-distance (135-315 km) movements by four adult females that were tagged with transmitters after nesting at Kamehame, Hawaii. All positions recorded were within sight of land. A fifth hawksbill equipped with a satellite transmitter after nesting on Maui traveled 240 km to the island of Hawaii (Ellis et al., in press).

Bass (1999) provided a comprehensive description of how molecular genetic studies can contribute to the understanding of the natural history of the hawksbill, particularly with respect to migratory behavior. Based on a review of previous genetic studies in the Caribbean (Bass et al., 1996; Bowen et al., 1996; Republic of Cuba, 1997) and a re-analysis of mitochondrial DNA sequence data from eight nesting populations, Bass (1999) concluded that there was considerable evidence that foraging ground populations of hawksbills are derived from multiple stocks that originate on distant nesting grounds. This finding was interpreted by the author as strong evidence that hawksbills migrate between nesting and foraging locations. Genetic data are now being gathered from hawksbills throughout the Caribbean, and it is likely that our understanding of their complex life histories and movements will improve significantly in the near future.

Conclusions

Data from tag-returns in the Caribbean region demonstrate that hawksbill turtles show dispersal and migratory behaviors similar to those of other species of marine turtles. Distances traveled may be long or short, depending on the respective locations of the developmental habitat, feeding ground, and nesting beach of individual turtles. Recapture data are too few at this point to discern patterns of movements for specific populations, but it is clear that the hypothesis that the hawksbill is "sedentary" must be discarded. A similar view is emerging in the Pacific Ocean where several long-distance movements by hawksbills have recently been documented (Miller et al., 1998). The percentage of hawksbills tagged in the Caribbean that have been recaptured internationally is within the range of that for other sea turtles that are considered to be highly migratory. Hawksbills migrate during several life-history stages, and these journeys may take them hundreds or thousands of kilometers across the sea and through the jurisdictional waters of many countries. Knowledge of the schedules and routes of these migrations is crucial to the effective management of hawksbills on both regional and multinational levels.

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