CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES
OF WILD FAUNA AND FLORA

HAWKSBILL TURTLES IN THE CARIBBEAN REGION:
Basic Biological Characteristics and Population Status

Summary

A compendium of information on marine turtles around the world was published nearly two decades ago, and subsequently reprinted with brief updates (Bjorndal, 1982, reprinted in 1995). More recently, an anthology of review articles on *The Biology of Sea Turtles* was published (Lutz and Musick, 1997), followed by a manual expounding standardized techniques for research and management (Eckert *et al.*, 1999). There have also been compilations of information on the hawksbill (e.g., Carr *et al.*, 1966; Witzell, 1983; Eckert *et al.*, 1999; Rhodin and Pritchard, 1999) as well as numerous individual projects.

Hawksbill turtles are highly complex, specialized marine reptiles. To complete the life cycle they require a diversity of environments, including terrestrial beaches, open ocean, coral reefs and coastal waters. Many of the biological characteristics of hawksbills discussed in this review can be treated together under a single concept: “late maturing and long-lived.” This incorporates considerations such as: fecundity, survivorship and recruitment, age structure, growth rate, and age at maturity.

Typically, they have a very high fecundity, or reproductive output: an average of 140 eggs is laid in one nest; several clutches are laid in one season; and nesting occurs during multiple seasons, although rarely annually. The high fecundity is offset by high mortality during early phases of the life cycle with probably less than one out of 1000 eggs surviving to adulthood. There are few studies of age structure, recruitment or survivorship at different life phases, but once a turtle reaches large size, and maturity, survival rate is potentially high, about 95% annually for some nesting females. Sex ratios are poorly understood, but they seem to be biased toward females.

Hawksbill turtle populations have numerous year-classes in a single population, with a relatively large numbers of immatures and relatively small numbers of adults. Several population models of marine turtles, including hawksbills, have shown that the large immatures and adults are especially important to the maintenance of a stable population (Crouse, 1999). This characteristic is shared with other late maturing and long-lived species, which as a rule are especially vulnerable to mortality, including exploitation, concentrated on large immatures and adults (Musick, 2001).

Linear growth rates vary between size classes and localities, but are slow enough to indicate that hawksbills take more than a decade to mature: the time from egg until returning to the same beach to breed for the first time may require between 15 and 40 years. However, there are considerable differences in growth rate between different areas, with fast growth (e.g. in Cuba and Mexico) influencing the age at which sexual maturity is reached, and also the intrinsic rates of increase and recovery times for depleted populations. Available evidence demonstrates that age of sexual maturity in hawksbills can extend beyond a single decade and possibly more than two.

Delayed maturity can serve as a “buffer”, so that although mortality is high – or even total – for several years, a stock of animals remains that will later mature and reproduce. However, species with low intrinsic rates of increase require considerable time to recuperate; hence, once reduced, it

may take decades for them to recover (Musick, 2001). In the middle or long-term any population of hawksbills subjected to sustained heavy mortality is vulnerable to collapse.

During a normal life cycle individual turtles disperse and migrate over long distances, often hundreds to over one thousand kilometres, moving onto the high seas, as well as into the territorial waters of different countries. Tagging studies and satellite tracking both indicate movement of hawksbills between feeding areas and nesting beaches. However, the same turtles may be sedentary and resident for long periods of time prior to and between reproductive migrations. There is also an indication of ontogenetic movement as Hawksbills grow and periodically change location.

Genetic analyses show that molecular markers (such as mitochondrial DNA haplotypes) can be used to distinguish among nesting populations. These studies, especially when coupled with data from tag returns, indicate that each nesting population forms a discrete demographic entity, genetically isolated from other populations. However, aggregations of hawksbills at foraging grounds and other non-reproductive areas present a mixture of haplotypes, indicating that turtles from distinct genetic stocks coexist on feeding grounds and other areas distant from the nesting grounds.

A wide variety of predators can prey on all life stages of hawksbills, but the most intense predation is on eggs, hatchlings, and small immatures. Hawksbill eggs and hatchlings on the beach are subject to predation by a wide variety of animals, including insects, crabs, lizards, birds, and mammals. Predation of hatchlings during the transit from the beach to offshore waters can be intense, involving sharks, bony fishes and marine birds. Even adult-sized hawksbills can be taken by tiger sharks (*Galeocerdo cuvieri*) and bull sharks (*Carcharhinus leucas*).

Hawksbills diet consists of soft-bodied invertebrates and sponges, that contain potent toxins, as well as glass spicules. Other than several highly specialized coral reef fishes, no other vertebrate is known to be able to tolerate such a noxious diet.

However, our understanding of the basic biology of hawksbills is incomplete, A major challenge is to comprehend the biological meaning of the many types of variation that occur among the diverse observations and measurements that are routinely made in these studies. Unfortunately, there is a paucity of long-term studies, and even for short-term projects, research methodologies are not always systematic or based on standardized techniques making comparison and interpretation of results difficult. In addition, most of the available information is based on monitoring of only one segment of the population – nesting females. Data from juveniles, males and non-nesting females is scarce.

In 1999, Meylan (1999a) estimated that a maximum of 5000 hawksbills nest annually in the Caribbean region, excluding Guyana, French Guiana, Suriname, and Brazil where a maximum of 600 hawksbills are estimated to nest.

Trends in hawksbill abundance over the last half-century (the maximum period for which regular monitoring data exist) are strongly decreasing and closely track the decline in the number of hawksbills represented in trade between Latin America/ Caribbean and Japan from 1970-86. In recent years, the number of nests documented annually at four nesting beaches (including the very large rookery in the Yucatan) show the potential for recovery of hawksbill populations.

The information on status, movements, reproduction, growth and present population trends all indicate that management and recovery of the species in the greater Caribbean area should be addressed on a regional basis. Some difficult questions must still be addressed including remaining uncertainties about the species' biology, equitable distribution of the costs and benefits of conserving the species and the harmonization of very different conservation perspectives and philosophies in the region.

Acknowledgements:
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Basic Biological Characteristics

Hawksbills, like other marine turtles, have a complex life cycle and it is important to appreciate that the specifics of each area, season and individual may vary greatly, (Frazier, 2001).

Each female leaves the sea, crawls up a sandy beach, and locates a nesting site above the level of the highest tide, typically within, or under, terrestrial vegetation. A female may make more than one attempt at digging a nest before successfully depositing a clutch of eggs in a chamber at least 10 cm and as much as 90 cm below the surface of the sand. Each egg weighs 25 g or more, and the average clutch has about 140 eggs (but sometimes there are as many as 250). After covering the nest, and having spent between 1 and 2 hours on land, she returns to the sea. At roughly 15-day intervals the same female will return, usually to the same stretch of beach, and nest again; this process will be repeated until she finishes nesting for the season, laying from 1 to 7 or 8 clutches. There is no parental care: the female leaves the eggs in the high beach to incubate on their own.

The time taken to hatch depends mainly on temperature, and may vary from 7 to 10 weeks. Incubation temperature also determines the sex of the embryos. After hatching, hatchlings may take several days to dig up and emerge from the nest, which usually occurs during the night. Once on the surface of the beach, they crawl down to the sea and swim out away from the shore. During their brief sojourn on land, the eggs/embryos/hatchlings are subject to various predators and other sources of mortality, such as compacting or erosion of the beach where the eggs have been deposited. To emerge from the nest and get into the sea as quickly as possible, hatchlings must make a series of unlearned “innate” responses to various stimuli. Each hatchling digs up, away from gravity, toward the top of the nest; it becomes inactive in the top layers of the nest if it encounters excessively warm temperatures; on emerging, it orients on the beach, moving toward that part of the horizon with the greatest light intensity, and usually with light of the shortest wavelength; at the same time, it moves away from objects and certain kinds of shapes on the horizon.

On reaching the water, each hatchling enters the beach surf, immediately diving through it. Once outside the surf, it swims offshore, usually heading into the waves. Hatchlings can evidently detect orbital movement, which allows them to orient into waves when they are on the surface and underwater, as well as in total darkness. After distancing themselves from the shore, hatchlings usually continue to maintain the same seaward heading that they took when leaving the beach, even if the angle into the waves is not the same as it was when leaving the shore. Apparently, during the initial stages of swimming away from the beach hatchlings can orient to the earth’s magnetic field. The compass heading that they select after arriving well offshore is evidently influenced by the heading that they take when leaving the nest and swimming out to sea, while orienting to light cues and/or waves (Lohmann *et al.*, 1997). Once offshore and into oceanic currents, the hatchlings may enter floating mats of jetsam (Bjorndal, 1997).

A number of years are evidently spent on the high seas, during which time at least some species of marine turtles disperse across ocean basins, circulating in ocean gyres. However, next to nothing is known about this phase of the hawksbill life cycle. When they have grown to about 20 cm in carapace length, at least in the Caribbean region, immature hawksbills begin showing up in coral reef areas, in what have been referred to as "nursery habitats." The turtles take up residency, evidently establishing a home range in which they feed, sleep and find refuge. The transition from pelagic to benthic waters involves a dramatic shift in habits, especially diet. Hawksbills, as the name indicates, have a hawk-like beak, which they use to bite and scoop out soft-bodied invertebrates from the reefs. In many localities their diet consists of select sponges, and involves regularly ingesting potent toxins, as well as glass spicules (Hartog, 1980; Meylan, 1988). Other than several highly specialized coral reef fishes, no other vertebrate is known to be able to tolerate such a noxious diet.

Like most other species of marine turtle, hawksbills are thought to pass through several nursery, or developmental habitats, but always residing in, or near to, coral reefs. After reaching sexual maturity, the turtles migrate from their feeding areas to nesting grounds. In some cases, this may involve directed movements of hundreds of kilometers, and results in at least the females returning to nest on the same beaches or area where they hatched. On laying her full complement of clutches for the season, the female migrates back to her foraging area. She will continue to make migrations between feeding and breeding areas every few years, for as long as she lives, which potentially could be several decades.

Fecundity:

Hawksbill clutches tend to be well above 100 eggs, and the largest clutches recorded for any turtle – 250 eggs - are from this species (Witzell, 1983); clutches of more than 200 eggs are not uncommon for hawksbills (e.g., Frazier, 1993; Chan and Liew, 1999; Dobbs *et al.*, 1999; Pilcher and Ali, 1999; Richardson *et al.*, 1999). There are indications that egg fertility (as determined by embryonic development visible to the naked eye) is inversely related to clutch size for hawksbills nesting on the Yucatan Peninsula. Hence, gross measures of fecundity (e.g., clutch size) may not be directly correlated to other ecological values fundamental to understanding the demography of these animals (Frazier, 1993).

The number of clutches an individual females lays per season can vary from 1 to 8 (Chan and Liew, 1999; Dobbs *et al.*, 1999; Pilcher and Ali, 1999; Richardson *et al.*, 1999), and the average number of clutches per season usually lies between 2 and 5 (e.g., Witzell, 1983; Chan and Liew, 1999; Mortimer and Bresson, 1999). In general, larger average values are reported when monitoring activities are long-term and involve thorough coverage of the nesting beach. Often "inter-nesting interval" (an average period between two consecutive nestings by the same season) is used to calculate the number of clutches per season. In cases where number of clutches per individual per season have been estimated on the basis of general records from a nesting season (not individual observations), the reported values are usually on the low extreme (e.g., Garduño-Andrade, 1999).

At Jumby Bay, Antigua, an 11-year study, based on saturation tagging in which close to 100% of the nesting animals are identified, was reported by Richardson *et al.* (1999). The Jumby Bay study (JB study) reported an average of 4.5 clutches (one of the largest reported averages), and a marked mode at 5 clutches per individual, per nesting season. With an average clutch size of 155 eggs, the seasonal reproductive contribution of a single female was calculated at 697.5 eggs using the average number of clutches per individual; using the modal number of clutches the estimate was 775.0 eggs per female, per nesting season. Considering an average population remigration rate of 2.69, the average individual *annual* fecundity was calculated at 288 eggs/female/year. It was further estimated that lifetime fecundity of a female (surviving for 8.1 years of non-annual nesting) would be 3,108 eggs (Richardson *et al.*, 1999).

Successful *repeated* reproduction by the same individual is a basic requirement for maintaining a *stable* population of animals like hawksbill turtles (Musick, 2001). One of the most detailed, long-term studies of hawksbills, at Cousin Island, Seychelles, has yielded results indicating that annual reproductive contribution of experienced females is significantly greater than for new recruits (Mortimer and Bresson, 1999).

Remigrations:
A term invented by marine turtle biologists, "remigration" refers to the return migration from feeding ground to nesting ground made by an individual that has already nested in a previous season. The remigration interval for hawksbills is usually reported to be between 2 and 4 years (Witzell, 1983), but can vary from 9 months (Pilcher and Ali, 1999) to at least 10 years (Mortimer and Bresson, 1999). The population mean, based on averaging the mean interval of each individual, was 2.69 years for Jumby Bay, Antigua and even though this was after an 11-year study, it was still considered to be an underestimate (Richardson *et al.*, 1999). Because these observations are dependent on identifying individual turtles, and this is normally based on tag recaptures, questions of tag loss and efficiency in nesting beach coverage are central to interpreting the data (e.g., Dobbs *et al.*, 1999; Pilcher and Ali, 1999

Survivorship/mortality:
There is very little systematic information on hawksbill survival, and most of it is limited to eggs and hatchlings in nests. Values of both hatching success (percent of the clutch that lives at least until hatching) and emergence success (percent of the clutch that lives at least to emerge from the nest) can vary tremendously between beaches and nesting seasons, and even on the same stretch of beach during the same period of time. However, for "natural" nests (those left *in situ*) the average hatching success is often above 80%, and emergence success is not much less (Witzell, 1983; Frazier, 1993; Dobbs *et al.*, 1999; Richardson *et al.*, 1999). Where management procedures involve moving eggs, these values are almost always lower, often by a considerable margin (Frazier, 1993; Marcovaldi *et al.*, 1999). Hatchlings in the sea are likely to suffer relatively high mortality, but to date no systematic studies for hawksbills have been reported.

The JB study, indicated an adult annual survival rate of 0.94. Annual survival of seasonal cohorts varied from 0.93 to 0.96, and although the difference between these values may seem to be small, it has major implications for demographic models. Although further monitoring will elucidate annual survival more clearly, the reported estimations of the JB study show that if a population is to remain stable, the average nesting female must not only live to reach sexual maturity, but she must also reproduce over a period of at least 9 years. Given that some females in the population will die before making the average reproductive contribution, these "early deaths" must be balanced by other females that will survive and reproduce for considerably longer than 9 years. Considering delayed time to maturity (see below), some members of the population are likely to survive for half a century or more (Richardson *et al.*, 1999). Based on the best demographic models available for marine turtles, high annual survival of large benthic immatures and adults is required to maintain a stable population (Heppell *et al.*, 1995).

Recruitment:
As with survival and mortality, very little systematic information is available on recruitment rates for any of the life phases of hawksbill turtles. Results from the JB study , indicated that each year between 13.3 and 25.6% of the annual nesters were new recruits, and that the annual rate of

population recruitment (for reproductive females) was 9%. Overall, it was estimated that less than one egg in a thousand survives to produce a reproducing adult (Richardson *et al.*., 1999).

Age structure:

Little systematic information is available on age structure of hawksbill populations. In Cuba, reproductive status of females caught during the annual harvest, (which is not exclusively directed to nesting females, but on the total population above a certain size), 1983-1993 was classified on the basis of degree of follicular development that indicated the smallest females with signs of maturity at 51–55 cm Straight Carapace Length (SCL) and around 50% of females appearing mature (Moncada *et al.*, 1999).

León and Diez (1999) found very dense aggregations of immature hawksbills, but almost complete absence of adult-sized animals at selected sites in Jaragua National Park/Cabo Rojo (JNP/CR), Dominican Republic. As other foraging areas in the Caribbean have both immature and adult-sized hawksbills, and various reports exist of sparse nesting as well as carcasses of adult-sized turtles found on sandy beaches in the park, León and Diez (1999) established that significant nesting occurred in the recent past. The complete absence of adults in JNP/CR led the authors to conclude that this resulted from either hawksbills using different developmental habitats at different phases in their life cycle or intense exploitation, focused on nesting animals.

Sex ratios:

As in the case of other species of marine turtles, there have been few studies of sex ratios of hawksbill turtles. León and Diez (1999) investigated an aggregation of immature turtles at Jaragua National Park, Dominican Republic, based on blood serum testosterone analyses. They reported that females were nearly 3 times as numerous as males (2.71: 1). Records from the hawksbill fishery in Cuba indicate that between 1983 and 1997 the catch was strongly biased toward females, with reported ratios routinely greater than 4:1 (Carrillo *et al.*, 1999). In contrast, a slightly male-biased sex ratio was reported from Mona Island, Puerto Rico, where the research was based on laparoscopic observations of gonads (Diez and van Dam, in León and Diez, 1999). Although female-biased sex ratios are well known in other marine turtle species, these results raise questions of whether hawksbills usually have an excess of females in their populations or if males and females have very different habits that result in females being more subject to capture.

A basic question relates to the accuracy of sex determination. A male without secondary sexual characteristics would be indistinguishable from a female. Moreover, use of “minimum breeding size” is not reliable for classifying an animal as mature, for a significant proportion of hawksbills reaches sexual maturity after growing to a size “considerably larger than average breeding size” (Limpus, 1992). In contrast, tail lengths of some nesting females could be misinterpreted as masculine (Dobbs *et al.*, 1999). In theory, the examination of gonads and blood testosterone levels are free from these problems (Wibbles *et al.*, 2000).

Home range and territoriality:

There has been evidence for decades that hawksbills on foraging areas occupy home ranges (Thurston, 1976; Frazier, 1984; see also citations in Starbird *et al.*, 1999). Distance between subsequent captures of immatures at Mona Island, Puerto Rico, averaged 0.45 km (StDev 0.66 km) (Van Dam and Diez, 1998). At Jaragua National Park/Cabo Rojo, Dominican Republic, recapture information from 34 individuals involved an average of 204.4 days (StDev 141.0, range 45-571) between capture events; distance between first and last capture varied from 0.60 to 1.55 km, and averaged 0.36 km (StDev 0.32 km) (León and Diez, 1999).

Studies of reproductive females at Buck Island, US Virgin Islands, indicate that between nesting events they take up temporary residence in specific shallow water areas within 3 km of their respective nesting beaches. Once a female finished nesting, however, she left the area around the nesting beaches (Starbird *et al.*, 1999), presumably to return to her usual non-breeding home range.

In addition to evidence from a variety of sources on foraging site fidelity, there are some indications for territoriality in hawksbills. Submarine observations made at different localities, such as the southern Great Barrier Reef, Australia (Limpus, 1992) and Fernando de Noronha, Brazil (Sanches and Bellini, 1999), indicate that hawksbills are usually solitary, while other species, such as green turtles, are often in small groups. Moreover, when two hawksbills were put together they would bite each other (Sanches and Bellini, 1999).

Migrations:

Flipper tagging: Mark and recapture analysis, based on flipper tagging, has been the basis for investigating dispersal and migration of hawksbill turtles. This method has been criticized because of the problems of tag loss (Mrosovsky, 1983; Witzell, 1998). Despite the shortcomings of this method, recaptures from flipper tagging provide a wealth of information on hawksbill movements and migratory patterns. A review of tag return data – mainly from nesting females tagged on nesting beaches - from the Caribbean by Meylan (1999a) reported that, besides movements within territorial waters, international migrations and displacements of hundreds of km, and sometimes up to 2,000 km were not unusual. As these results can only be reported as point of tagging and release to point of recapture, the actual routes taken are unknown. Other reports of flipper tag recoveries indicate shorter distance movement; for example, hawksbills tagged in Cuba have been recaptured only within Cuban waters (Moncada *et al.*, 1998; Manolis *et al.*, 2000). Nonetheless, in all countries in the Greater Caribbean (*sensu* SPAW Protocol/Cartagena Convention) where hawksbills have been either tagged or recaptured from other tagging programs, there has been at least one international tag return (Figure 1).

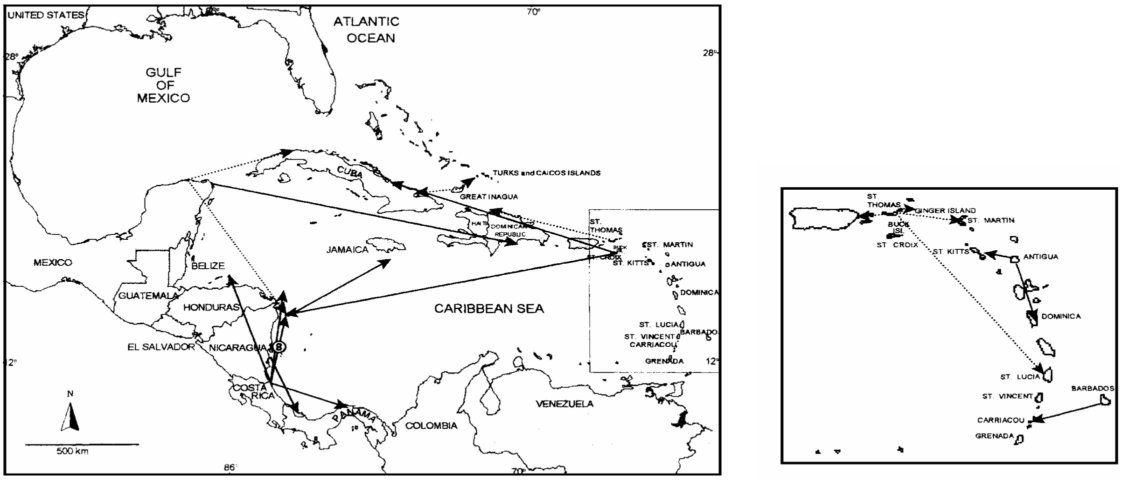


Figure 1. International displacements of hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean, based on recoveries of metal flipper tags. Solid lines represent adult turtles; dashed lines immatures (from Meylan, 1999a: figure 1).

Telemetry studies: Radio telemetry has been used with marine turtles, to investigate relatively short term movements over relatively short periods of time. Studies at Buck Island, U.S. Virgin Islands, indicate that although nesting hawksbills stay within about 3 km of the island's nesting beaches between nesting events, as soon as they have finished nesting for the season they migrate out of the area immediately (Starbird *et al*., 1999). Because of the limitations of VHF radio telemetry, once a transmitter is out of range, the position and condition of the study animal becomes unknown.

Satellite telemetry provides an estimate of the track taken by the "instrumented" turtle, with the caveat that the amount of data from satellite tracking studies is frequently limited to the few months of equipment function and routinely represents only a portion of the track taken by the study animal. Preliminary data are now available for 47 satellite telemetry tracks of hawksbills in the Caribbean, which were initiated in ten different countries and territories, and involved 40 post-nesting females, one male, and six other animals (Tables 1 and 2). Although sample sizes are generally small, and vary greatly between countries: from 1 in Belize, to 14 in Cuba, interesting patterns are beginning to emerge.

Table 1. Results from recent studies of just post-nesting migrations by female hawksbills in the Greater Caribbean using satellite tracking and estimated area of coral reef for each country where satellite tracking studies were initiated* (adapted from Frazier, 2001)

Site of nesting and tagging	Approximate point to point displacement (km)**	Source of data	Estimated reef area at tagging site*** (km^2)
Antigua & Barbuda	25	B.Schroeder & G.Balazs, pers. com.	240
Antigua & Barbuda	25	B.Schroeder & G.Balazs, pers. com.	240
Antigua & Barbuda	100	B.Schroeder & G.Balazs, pers. com.	240
Antigua & Barbuda	900	B.Schroeder & G.Balazs, pers. com.	240
Barbados	200	Horrocks et al., 2001	100
Barbados	285	Horrocks et al., 2001	100
Barbados	335	Horrocks et al., 2001	100
Barbados	435	Horrocks et al., 2001	100
Belize	50	B.Schroeder & G.Balazs, pers. com.	1,330
Costa Rica****	290	CCC, unpublished data	970
Costa Rica****	470	CCC, unpublished data	970
Cuba, Doce Leguas	< 50	Prieto et al., 2001	3,020
Cuba, Doce Leguas	< 50	Prieto et al., 2001	3,020
Cuba, Doce Leguas	< 50	Prieto et al., 2001	3,020
Cuba, Doce Leguas	< 50	Prieto et al., 2001	3,020
Cuba, Doce Leguas	< 50	Prieto et al., 2001	3,020
Cuba, Doce Leguas	1000	Prieto et al., 2001	3,020
Cuba, Doce Leguas	1000	Prieto et al., 2001	3,020
Jamaica	50	B.Schroeder & G.Balazs, pers. com.	1,240
Jamaica	50	B.Schroeder & G.Balazs, pers. com.	1,240
Jamaica	650	B.Schroeder & G.Balazs, pers. com.	1,240
Jamaica	1,100	B.Schroeder & G.Balazs, pers. com.	1,240
México****	160	Garduño et al., in prep.	1,350
México****	260	Garduño et al., in prep.	1,350
México****	260	Garduño et al., in prep.	1,350
México****	340	Garduño et al., in prep.	1,350
Nicaragua****	145	Lagueux & Campbell, unpubl.	710
Nicaragua****	145	Lagueux & Campbell, unpubl.	710
Nicaragua****	155	Lagueux & Campbell, unpubl.	710
Nicaragua****	435	Lagueux & Campbell, unpubl.	710
Puerto Rico	490	C. Diez, pers. com	480
Puerto Rico	550	C. Diez, pers. com	480
Puerto Rico	1,450	C. Diez, pers. com	480
Puerto Rico	1,670	C. Diez, pers. com	480
US Virgin Is	80	Hillis-Starr et al., 2000	200
US Virgin Is	110	Hillis-Starr et al., 2000	200

* not included in this table are data for seven hawksbills, including one male, tagged in various locations in Cuba, as well as four post-nesting females tagged in Mexico by Byles and Swimmer (1994).

** if the "precise distance" is not available from the source, an estimated value from map readings is indicated; given the levels of precision for satellite telemetry, values are rounded to the nearest value of 5 km.

*** from Spalding et al. (2001).

**** only coral reef data for Atlantic coasts are considered

Of four females that nested on the Yucatan Peninsula, Mexico, and outfitted with satellite transmitters, two swam to the Campeche Banks where they stayed, and two others swam out into international waters in the Gulf of Mexico and Caribbean (Byles and Swimmer, 1994). Four other hawksbills tagged with satellite transmitters after nesting (Garduño *et al*.., in prep.,) remained on the Campeche Banks, traveling less than 350km from where they had nested.

Of seven nesting females tagged with transmitters in Doce Leguas, Cuba, five stayed within 50km of the nesting beach, and the remaining two traveled as far as the coast of Honduras (about 1,000km; Prieto *et al*.., 2001;). In another study, seven hawksbills from Cuba were tracked and four of these passed through the territorial waters of the Cayman Islands, Belize, Honduras, Nicaragua, Colombia, Jamaica, Mexico, and an area near Antigua/Guadeloupe/Montserrat, traveling distances as much as 2,450 km. Three others hawksbills fitted with satellite transmitters did not leave Cuban waters (Carrillo *et al*.., 1999; Manolis *et al*.., 2000; Prieto *et al*.., 2001; Webb, pers. com.).

In Barbados, four female hawksbills were tracked through periods varying between 7 and 18 months during which they each emigrated to territorial waters of a different country: Dominica, Grenada, Trinidad and Tobago, and Venezuela,. Three of these hawksbills spent time on the high seas, outside the territorial waters and Exclusive Economic Zone of any State (Horrocks *et al*.., 2001).

Two post-nesting females, tagged at Mona Island, Puerto Rico, traveling the greatest distances, arrived in Rosalind Bank, Honduras and Miskito Cays, Nicaragua and, while two others only went as far as the Turks & Caicos and St. Barts, Guadeloupe (French Antilles). In three cases there was a certain period on the high seas (Diez, in prep.). Two females at Buck Island, US Virgin Islands, only traveled distances of about 80 and 110 km, going to the British Virgin Islands and Puerto Rico (Hillis-Starr *et al*.., 2000).

Additional recent work has provided information from several other sites in the Caribbean (Schroeder and Balazs, pers. com.). At Jumby Bay, Antigua, two of four nesting females did not leave Antigua while one of them traveled to St. Christopher and Nevis. One nesting female in Belize had a track that went about 50 km, not leaving Belician waters. One of four nesting females in Jamaica was reported to travel to Belize another to Honduras. In addition, three of these animals spent time on the high seas. Finally, of four nesting females tagged with satellite transmitters in Nicaragua; one of them moved to the border with Honduras, while the others did not leave Nicaraguan territorial waters (Lagueux and Campbell, unpubl.)

In interpreting migration, it should be borne in mind that most of these data only concern adult nesting females (and some males), and that these only form a small proportion of the total population, possibly only 5 % (ROC 1998, 2000), and may not be typical of other life stages.

When interpreting results from satellite tracking it is important to note that the "last position" received is not necessarily the last position where the animal went (or was headed) in its emigration. For example, for countries where data from both conventional flipper tagging and satellite telemetry are available, some of the flipper tag returns (which are only point-to-point, and cannot account for the actual distance of the journey made) are far greater than the longest satellite tracks. The ratios of greatest distances for flipper tag and satellite transmitter studies are 1.8:1 for Costa Rica, 4.7:1 for Mexico, 6.3:1 for Nicaragua, and 18.3:1 for US Virgin Islands (Table 2).

Table 2. Longest records for displacements of post-nesting hawksbill turtles in the Caribbean, comparing data from flipper tag recoveries and satellite telemetry tracks from the same country.

Country where tagged	Flipper tag		Satellite telemetry track		Ratio – Flipper:Satellite
	Longest record (km)	Source	Longest record (km)	Source	
Costa Rica	850	[1]	470	[2]	1.8 : 1.0
Mexico	1,622	[3]	345	[4]	4.7 : 1.0
Nicaragua	628	[5]	100	[6]	6.3 : 1.0
US Virgin Is.	2,000	[7]	110	[7]	18.3 : 1.0

Sources: [1] Bjorndal *et al.*, 1993: in Meylan, 1999a; [2] <http://www.cccturtle.org/sat_tort_all.htm>; [3] Márquez 1990: in Meylan, 1999a; [4] Garduño, pers. com.; [5] Nietschmann, 1981: in Meylan, 1999a; [6] Schroeder & Balazs, pers. com.; [7] Hillis-Starr *et al.*, 2000.

Information from all 47 of the available satellite tracks mentioned above showing where the turtles were tagged with satellite transmitters and the various countries that they visited after being released is contained in Annex I. In some cases, such as Barbados, Costa Rica, Puerto Rico, and US Virgin Islands, the animals sampled seem to leave the breeding area fairly directly. In other cases, such as Belize, Cuba, Mexico, and Nicaragua, most of the animals sampled seem to stay within national waters. However, in all cases (except Belize which had a sample size of only 1) the satellite telemetry tracks showed that there was at least some degree of extra-territorial dispersion.

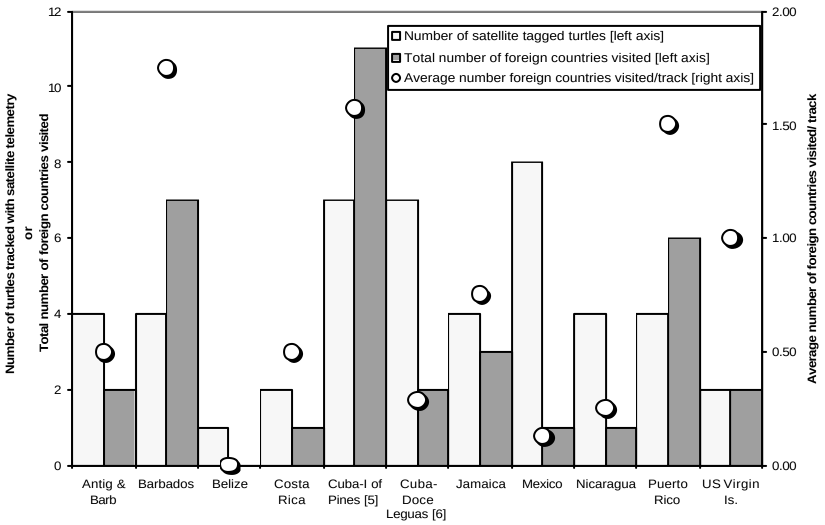


Figure 2. Country-by-country comparison of satellite telemetry studies in the Greater Caribbean showing numbers of hawksbills tagged with transmitters, and two indices of the level of post reproductive dispersal (results from Cuba include [5] one male and six other animals from Isla de Pinos and other localities, and [6] seven post-nesting females from

Tracks of hawksbills from some countries are notable for the number of "visits" that are made *en route (*Figure 2*)*. On average, a Barbados turtle made three visits during a track, and in the case of Barbados, the average number of visits to foreign countries was also three. Because some turtles tagged in Barbados visited the same foreign countries, the overall average of the number of foreign countries visited for all four tracks from Barbados was 1.75. Considering just post-nesting females, Puerto Rico, Jamaica, and the US Virgin Islands also show the high levels of foreign post-reproductive dispersion, with values for average number of foreign visits/turtle at 2.00, 1.50, and 1.0, respectively. The average number of foreign countries visited per track for these same three

territories was 1.25, 0.75, and 1.00, respectively. In contrast, Cuba, Mexico, and Nicaragua show low levels of foreign post-reproductive dispersion, with average number of foreign visits per turtle at 0.57, 0.25, and 0.25, respectively, while the values for average number of foreign countries per track were 0.29, 0.13, and 0.25, respectively. Antigua & Barbuda and Costa Rica show intermediate values.
In addition to the seven nesting females from Doce Leguas, seven other animals (including a male) were instrumented with satellite transmitters in Cuba. In contrast to the results from females at Doce Leguas, these animals showed a high level of dispersion to foreign destinations, with average number of foreign visits per turtle at 1.71 and average number of foreign countries per track at 1.57 (Table 3).

Based on the satellite telemetry, "visits" are most common in Honduras, Nicaragua, and the high seas (Table 3). However, here again the effect of small sample size is apparent. None the less, although satellite telemetry studies with hawksbills were carried out in just 10 countries, the satellite telemetry tracks passed through 24 countries, as well as the high seas.

Satellite tracking has provided information on the movement of adult nesting females during the period they are near a nesting beach, and the period after they complete nesting. The generalised results from 36 post-nesting females (Table 1) in the Caribbean are:

- After completing nesting, females leave the nesting beach and appear to return to sites at which they live (versus those at which they nest). The results suggest adult females are reasonably sedentary in the areas in which they live, feed, grow and maintain themselves, and that the longer distance movements are mainly associated with nesting each 2-4 years.

- The route taken may or may not be direct, but the speed at which the return takes place is often fast (20-40 km per day). The routes taken to and from nesting areas may involve travel through international waters and through the territorial waters and exclusive economic zones of a number of nations, given their close proximity to each other in the Caribbean.

- Tracking results from individuals for over 1 years duration indicate adult females continued to live in the areas they reached, with home ranges of 2 to 50 square kilometres.

- The distance between nesting areas and living areas as known to date, from the 36 individuals, are broadly as follows.

<100 km	33%
101-500 km	44%
501-1000 km	14%
1001-2000 km	8%

Hawksbill migrations and coral reef areas: In an attempt to explain apparent differences in levels of post-reproductive dispersal, Prieto *et al..*, (2001) suggested that the availability of foraging habitat in the vicinity of nesting beaches may be a deciding factor. Although current knowledge of the distribution, amount and quality of hawksbill foraging habitat in the Caribbean, or elsewhere, is extremely limited, the estimated area of coral reef in different countries can be used as an index to test this hypothesis. Results of satellite tracking report that, in cases where there are apparently extensive reef areas near to nesting beaches, a proportion of post-nesting females may remain in relatively close proximity to their respective breeding areas (e.g., Cuba, Jamaica, and Mexico) yet a portion of the post-nesting females may still make migrations of hundreds, or over a thousand km.

Immatures and males: It is important to emphasize that the previous discussion is focused almost exclusively on post-nesting females; very few adult males or immatures of either sex are included. The migratory behavior of hawksbills may differ between sexes in mature turtles, and also between life stages. For example, van Dam and Diez (in prep.) used light-sensitive transmitters to track adult males at Mona Island (Puerto Rico) and they found that three of males did not appear to move out of the area after the breeding season, suggesting that they may be year-round residents of the island (Diez pers. com.). Most reports on flipper tagging describe high local recapture rates of immatures in the Caribbean region (e.g., Nietschmann, 1981; Boulon, 1994; Garduño and Márquez, 1994; ROC, 1998; van Dam and Diez, 1998; reviewed by Meylan, 1999a), and it is likely that in general, immature hawksbills exhibit strong site fidelity on their feeding grounds, tending to remain in one developmental habitat for an extended period, before moving on to other developmental habitats (Limpus, 1992; Van Dam and Diez, 1998). Nonetheless, movements of immature hawksbills can also be extensive, exhibiting displacements of hundreds of kilometers; for example, two immatures tagged in Yucatán, Mexico, dispersed minimum straight-line distances of 560 and 900 km, arriving in Cuba and Nicaragua, respectively (Garduño, in Meylan, 1999a), and two other immatures tagged in the US Virgin Islands traveled minimum straight-line distances of 650 and 720 km, arriving in St. Lucia and Dominican Republic, respectively (Boulon in Meylan, 1999a).

Summary: Summarizing the available information on flipper tagging and satellite telemetry (Annex I) shows that there are recapture/tracking data from only 11countries that have initiated tagging studies and of these only Costa Rica, Cuba and Mexico each tagged more than ten hawksbills that were subsequently recaptured or tracked. The reports of recapture sites and territories visited during different migration tracks show a web of complex regional movements involving 29 countries and territories in the Greater Caribbean. Of these (and discounting the high seas), Cuba, Honduras, Mexico, and Nicaragua stand out as the most frequent destinations for migrating hawksbills. For example, hawksbills tagged in Cuba have been caught in, or passed through: Belize, Cayman Island, Colombia, Cuba, Honduras, Jamaica, Mexico, Nicaragua, and an area near Antigua/Guadeloupe/Montserrat; one individual after leaving Cuba traveled to Honduras, Nicaragua, and Colombia before transmissions ended (Manolis *et al*.., 2000). Hawksbills tagged in Mexico have gone to Cuba, Dominican Republic, Mexico, and Nicaragua, while hawksbills in the US Virgin Islands have traveled to British Virgin Islands, Cuba, Dominican Republic, Nicaragua, Puerto Rico, and St. Lucia. On the other hand, there are also many records that indicate short distance movements. In the case of Cuba, nearly 50% of the records of satellite track visits of hawksbills tagged in Cuba are from within Cuba itself, and for post-nesting females the proportion is as high as 71% (Prieto *et al*.., 2001); for Mexico 75% of the post-nesting females were last recorded in Mexican waters.

Although the available data are too limited to enable a robust estimation of the proportion of juveniles or adult male turtles that immigrate and emigrate to and from the territorial waters of any single country, they show that adult female hawksbill turtles can migrate and disperse over a large area.

In the particular case of the Greater Caribbean, the average distance of post-nesting migrations is approximately 370 km. In an area such as the Greater Caribbean, with island nations that are relatively close to one and other, this average post-nesting migration distance would typically involve crossing international borders.

Although emphasis in this summary has been placed on areas to which hawksbills seem to migrate and concentrate after reproduction, and large foraging areas are clearly essential for the survival of the species, breeding areas are no less critical, even if the turtles are spending a relatively short period of time there. For example, the apparently rapid departure of post-nesting females from Barbados, US Virgin Islands, and many other nesting beaches, does not mean that these relatively small breeding localities are of limited importance to Caribbean hawksbills. .

Genetic studies:

Bass (1999) reviewed results from research on mitochondrial DNA (mtDNA) sampled from hawksbills at eight nesting areas and two foraging areas and concluded that nesting populations in the Caribbean are genetically distinct in terms of unique mtDNA haplotypes or haplotype frequency shifts. This is evidence of low rates of gene flow between nesting populations and results in population units that are genetically isolated. Hence, each nesting population exists independently of others, regardless of the geographic distance between them, and the size and composition of one population is little influenced by immigration of turtles from other populations. At the same time, genetic studies of hawksbills found on foraging grounds in Cuba and Puerto Rico indicate that in both cases the feeding "population" is composed of aggregations of individuals from at least six different nesting grounds , but in the case of the Cuban foraging population it is very clear that it is drawn primarily from the Cuban nesting population (67%), although Bass adds that this conclusion does not preclude the possibility that animals from other nesting locations also forage in Cuban waters (Table 3). Bass concluded that although studies to date had only included a few sites, the finding of mixed stocks at foraging areas could be extrapolated to other localities on the basis of what is known from tagging projects

Table 3. Estimates of contributions from different nesting populations of hawksbill turtles (*Eretmochelys imbricata*) to two non-reproductive aggregations in the Caribbean, based on mtDNA haplotypes. The values presented should NOT be used as precise values, but rather as qualitative estimates of the composition by stocks at foraging sites (taken from Bass, 1999: Tables 1 and 2).

Inferred Nesting Population	Foraging area			
	Cuba (n = 55)		Puerto Rico (n = 133)	
	Contribution	Std. Dev.	Contribution	Std. Dev.
Antigua	0.05	0.05	0.04	0.03
Barbados	0	0	0	0
Belize	0.08	0.07	0.03	0.03
Cuba	0.67	0.09	0.24	0.05
México	0.05	0.03	0.14	0.03
Puerto Rico	0.06	0.03	0.14	0.04
US Virgin Is	0.09	0.09	0.42	0.06

Note: Where standard deviations are relatively large (close to or larger than the value for contribution) the value for the contribution is unreliable (Bass, 1999).

Díaz-Fernández *et al.*. (1999) analyzed samples from nesting and foraging areas in Cuba, Mexico and Puerto Rico. Using larger sequences of the mtDNA for analysis, they were able to subdivide two of the haplotypes described by Bass *et al.*. (1996) into 2 and 3 haplotypes, respectively. In addition, Díaz-Fernández *et al.*. (1999) studied samples not available to Bass *et al.*. (1996) that were from a more geographically diverse and larger number of hawksbills. Although there are differences in the results of the two studies, Díaz-Fernández *et al.*. (1999) confirmed the general conclusions of Bass: each nesting population has a distinct haplotype composition, and each non-reproductive area contains a mixture of haplotypes (Table 4).

Table 4. Estimated percent contribution of Cuban, Mexican, Puerto Rican and unknown nesting populations to aggregations of hawksbill turtles (*Eretmochelys imbricata*) in non-reproductive areas in Cuban, Mexican, and Puerto Rican waters, as deduced from mtDNA haplotype composition (from Díaz-Fernández et al., 1999: Table 4). The Cuban sample is broken into three fishing areas, which are further subdivided into specific localities and/or seasons; figures in bold represent pooled results for each fishing area or country outside of Cuba.

	SAMPLE	NESTING BEACH HAPLOTYPE CONTRIBUTION (%)			
FORAGING SAMPLE	SIZE (n)	Cuba	Mexico	Puerto Rico	Unknown
CUBA					
Southeast	44	70	7	12	11

Doce Leguas-94	23	83	4	4	9
Doce Leguas-96	13	54	15	8	23
Santa Cruz	8	63	0	38	0
Southwest	115	46	10	30	14
Isla de Pinos-spring	40	33	15	40	12
Isla de Pinos-autumn	75	53	7	25	15
Northeast	59	42	14	31	13
Nuevitas	17	41	12	29	18
Las Tunas	15	33	7	33	27
Cayo Romano	9	34	33	33	0
Others	18	56	11	28	5
MÉXICO Ria Lagartos	21	0	71	5	24
PUERTO RICO Mona Island	106	29	10	41	20

Statistical comparisons between haplotype identities and compositions at foraging and nesting sites allows estimates of relative contributions by rookeries at sites where various stocks aggregate (such as in foraging sites). Diaz-Fernández *et al..*, (1999) reported that the greatest contribution of haplotypes at foraging areas in Puerto Rico and in Cuba was from local nesting populations. Differences at the same foraging locality were reported for different seasons (Díaz-Fernández *et al..*, 1999). For example, the contribution of Cuban nesting haplotypes at a non-reproductive area around Isla de Pinos increased from 33% in spring to 53% in autumn. Large variation was also reported between different years: the percent contribution of Cuban nesting beach haplotypes in Doce Leguas foraging samples dropped from 83% in 1994 to 54% in 1996. Values also varied between different non-reproductive localities (i.e., fishing area) in the same country (Table 4).

Bass (1999) cautioned that percent contribution values derived from current statistical analyses of Caribbean hawksbill genetic surveys should be interpreted as qualitative indications and not as precise estimates of genetic composition. More precise conclusions will only be possible after a regional inventory of haplotypes is completed, including identification of source populations of some observed haplotypes, and better understanding is derived about how, where, and which populations mix and sort in time and space. Increasing the geographic scope in the hawksbill genetic surveys among Caribbean rookeries is clearly a gap that needs to be filled in order to improve our understanding of the species´ migratory habits in the region.

The results of the genetic studies are consistent with various other lines of research, particularly tag returns and migration studies. Taken together they show that each nesting population behaves as a distinct management unit, despite the fact that the individuals disperse, migrate, and live within an expanse that may include different sovereign territories. The contribution of different nesting populations at a specific foraging ground can be subject to change between different seasons and different years.

Hybridization:

Hawksbills are involved in many of the cases of hybridization known between marine turtle species. Hybrids between hawksbills and loggerheads (*Caretta caretta*) have been reported from Bahia, Brazil, where there are indications that the hybrids were at least second generation (Conceição *et al..*, 1990; Bass *et al..*, 1996; Bass, 1999; Marcovaldi *et al..*, 1999). A hybrid between a hawksbill male and a loggerhead female was reported from Florida, USA, and an egg collected in Surinam produced a hybrid identified to have come from a male hawksbill and a female green turtle (*Chelonia mydas*), and thought to have been second (or later) generation (Karl *et al..*, 1995).

Growth rate:

Growth rates of hawksbills are thought to be influenced by a variety of "internal" factors such as age/body size, sex, and genotype of the turtle (Limpus, 1992; Boulon, 1994; Chaloupka and Limpus, 1997), as well as "external", or environmental, factors such as food quality and quantity, competitors, predators, ambient temperature, latitude, etc. (León and Diez, 1999). Even at a general level, it is not yet clear how environmental and physiological variables act, either singly or in concert, to affect the growth of the turtles. Moreover, different growth rates of individuals exploiting sites of differing quality in the region will have profound repercussions on other parameters of importance to population dynamics, such as the rate of sexual maturation, and even rates of recruitment if individual stocks utilize different foraging or developmental habitats with variable qualities.

Capture and recapture studies on wild, free-ranging hawksbills have used linear growth increments (the difference in carapace length measured at capture and recapture events) to estimate growth rates. Results with immature hawksbills can be quite variable between studies. There is a strong tendency for the smaller animals to grow faster (Annex II, Figure 5), a finding that is repeated in diverse geographic areas, as well as in other species of marine turtles. There are also differences among different regions, and even localities in the same region. For example, hawksbills from Mona Island, Puerto Rico (Diez and van Dam, 1997) are rarely reported to grow more than 3 cm/year while reported linear growth rates can be much higher - more than 6 cm/year in the faster growing size classes, at St. Thomas, US Virgin Islands (Boulon, 1994), and more than 7 cm/yr in Lanza Zó, Dominican Republic (León and Diez, 1999), Doce Leguas, Cuba (Carillo *et al.*., 1998; CCMA, 1998; Prieto *et al.*., 2001; ROC, 1998, 2000), and Ria Lagartos, Mexico (Garduño, unpublished).

Adult hawksbills: There are a variety of reports on "growth rates" of adult hawksbills (e.g., Limpus, 1992; Dobbs *et al.*., 1999; Pilcher and Ali, 1999), but these need to be interpreted with caution. Routinely, the standard errors reported in each of these studies with adults are greater than the respective means, raising questions about the usefulness of the statistical values. As in other marine turtles and reptiles, linear growth in hawksbills that have reached sexual maturity is asymptotic: consistently slow, if at all detectable.

There have been few reports of linear growth rates of hawksbills in the Greater Caribbean that were at least as large as the smallest average size at which nesting females have been recorded (e.g. 80 cm straight carapace length or more). In their detailed study, Diez and van Dam (2002) found that three females at Monito Island between 80 and 89 cm had an average linear growth rate of 1.33 (± 0.36) cm/yr, while a fourth female at Mona Island reef showed a calculated change in length of – 0.29 cm/yr. It is unclear if these Puerto Rican turtles were confirmed to be adults: that is, if they were reproducing. Marine turtles, like many other reptiles, do not all become adult (i.e., reach reproductive maturity) at the same body size, and it is not uncommon to find turtles *larger* than the average size of breeders that have not reached reproductive maturity (Limpus *et al.*., 1994); hence, body size alone cannot be used as a totally reliable indicator of maturity. There are two reports of linear growth rates of nesting females in the Caribbean (Annex II): eight turtles between 80 and 89 cm, measured in Doce Leguas, Cuba, showed an average growth rate of 0.83 (± 0.98) cm/yr (Moncada and Nodarse, unpublished), and nine nesting females between 85 and 95 cm from Ria Lagartos, Mexico were reported to have an average linear growth rate of 0.34 (± 0.26) cm/yr (Garduño *et al.*., unpublished). These results - with the standard deviation larger than, or nearly as large as, the mean - are usual for adult animals. They show that growth is so slow that it may be insignificant, and the statistics are of limited use.

Immature hawksbills: Using publications (Carrillo *et al.*., 1998) and recently acquired, unpublished data, and standardizing measurements between studies so that the results are expressed in the same terms, more extensive comparisons can now be made (Annex II). The data show considerable variation between studies in different localities. Moreover, there are marked differences in average growth rates between turtles from localities that are no more than 6 km apart. As in earlier studies, Diez and van Dam (2002) reported that the growth rates of immature hawksbills in the 30-39 cm size class were generally the fastest. Data from 41 individuals, and 101 growth increments, showed that individuals in this size class at Mona Island “reef,” had an average growth rate of 3.07 (± 1.77) cm/yr; at Mona Island “cliff,” 31 other turtles with 80 growth increments, yielded a very similar result: an average of 3.17 (± 1.77) cm/yr. Yet, at Monito Island “cliff wall” (a site just 6 km from the former), data from 24 turtles and 40 growth increments produced an average growth rate for the same size class that was nearly twice as fast: 6.47 (± 3.44) cm/yr. (In addition to the larger mean at Monito, there is also a significantly larger variance [F 40, 101 = 3.78; p<0.001], indicating that some of the Monito animals were growing at an extremely fast rate, while others may have been growing at rates no different from what was found at Mona). A similar phenomenon was reported from the Dominican Republic, with hawksbills of the same 30-40 cm, fast-growing size class. Léon and Diez (1999) reported that five individuals at Cabo Rojo, Muelle Oeste, or Playa Oesta had an average growth rate of 4.04 (± 1.62) cm/yr, while five other turtles at Lanza Zó (less than 15 km from the other study sites) had an average growth rate of 8.84 (± 1.25) cm/yr. The reasons for these marked differences in growth rates between localities that are relatively close are not known, but are thought to be related to food availability and quality at different reef localities in the waters of Puerto Rico and the Dominican Republic, respectively.

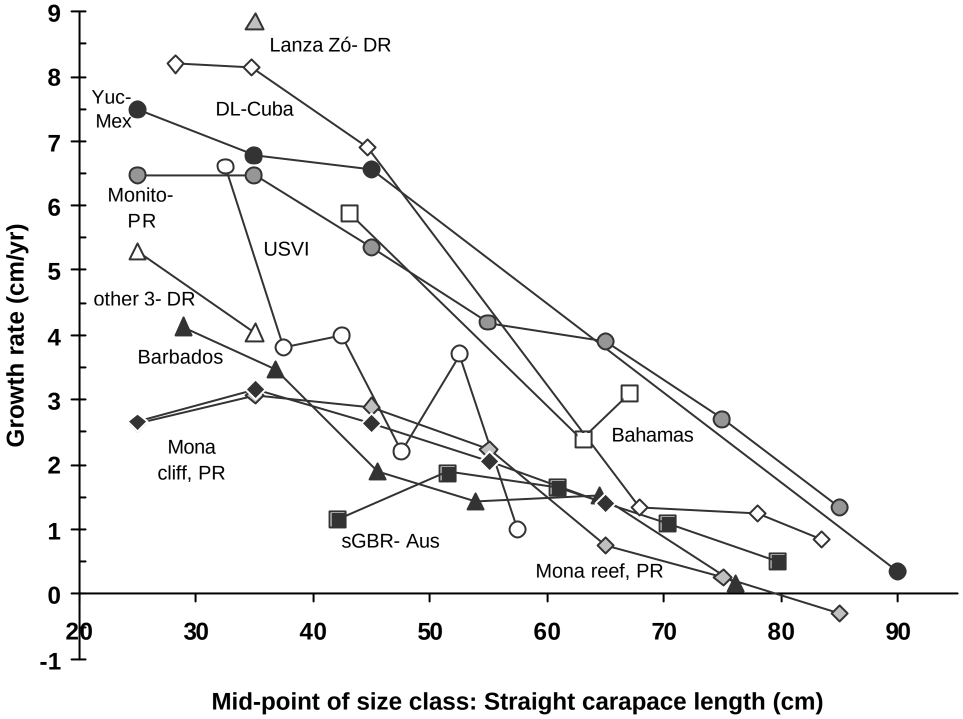


Figure 3. Relationship between linear growth rate (cm/yr) and midpoint of size class (in SCL) for wild hawksbill turtles at 11 localities: Bahamas; Barbados= West Coast bank reef, Barbados; DL-Cuba= Doce Leguas Keys, Cuba; Yuc-Mex = Ria Lagartos, Yucatan, Mexico; Lanza Zó-DR = Lanza Zó, Dominican Republic; other 3 - DR = Cabo Rojo, Muelle Oeste, Playa Oeste in Jaragua National Park/Cabo Rojo, Dominican Republic; USVI = St. Thomas, U.S. Virgin Islands; Mona cliff = Mona Island cliff, Puerto Rico; Mona reef = Mona Island reef, Puerto Rico; Monito-PR = Monito Island, Puerto Rico; sGBR-Aus = southern Great Barrier Reef, Australia. The curved carapace lengths for sGBR were transformed to SCL using SCL= 0.939(CCL) - 0.154, kindly provided by T. Redlow, Florida Sea Turtle Stranding and Salvage Database. See Table 5 for details and sources of original data

Despite the diversity of the results, there are some clear general tendencies; the relationship between size class midpoint and average linear growth rate (Figure 3) shows that linear growth rate declines with increasing body size. In one study (Mexico) the decline appears to be more or less steady, in five other cases (Cuba, Mona Island cliff, Mona Island reef, Monito Island, and Australia) there is a slight increase (or no change) at first, followed by a steady decline (see discussion below, on "polyphasic" growth), while in three other sites the trend is irregular, sometimes tracing a zigzagged line (e.g., Bahamas, Barbados, and St. Thomas) (the values for the Dominican Republic, with only one and two points, respectively, are too limited to determine a trend).

In evaluations of the variety of different linear growth rates from Caribbean hawksbills, there have been suggestions that the turtles have two distinct types of growth: fast and slow (Carrillo *et al*.., 1998; Prieto *et al*.., 2001). The trend lines in Figure 3 appear to generally fall into an upper group (Bahamas; Cuba - combined data; Dominican Republic – Lanza Zó; Mexico – Yucatan; and Puerto Rico – Monito), and a lower group (Barbados – west coast; Dominican Republic – combined data from Cabo Rojo, etc.; Puerto Rico – Mona Island cliff and Mona Island reef; and Australia – southern Great Barrier Reef. In general, the growth rates in the upper extreme are twice or more those in the lower extreme. However, there is no unequivocal separation between these groups. The trend lines from Bahamas and Cuba both make incursions into the lower cluster, and the line for the US Virgin Islands zigzags between the upper and lower extremes of the graph.

Diez and van Dam (2002) detected polyphasic growth at their Mona and Monito Island study sites, with the fastest growth spurt occurring in the 34-35 cm size class. The Cuban and Mexican data presented in Figure 3 stand out as apparently showing monophasic trends, with more or less steady declines in the trend lines. However, in the former there are no values in the 50-59 cm size class, and in the case of Mexico there are no values between the midpoint for the 40-49 size class and nesting females. The data from Barbados show a similar trend, with growth rate continually decreasing from the 20-29 cm cm size class. However, when the trend line is plotted from growth increments measured over a period of at least 12 months (not 6 months as shown in Figure 3), the form is different, with an increase between the 20-29 cm and 30-39 cm size classes, followed by a more or less steady decline. The other studies from the Caribbean (Bahamas, Dominican Republic, and US Virgin Islands) are compromised by relatively small sample sizes, so a more detailed interpretation would not be meaningful. It is unclear why not all of the Caribbean studies show clear polyphasic growth functions, but certainly limited sample sizes reduce the robustness of the generalizations for a number of the studies. In addition, as shown in the case of Barbados, when growth increments are based on periods of at least 12 months, the trend line can change considerably. Given the risks of basing long-term trends on short-term values and variability from seasonal effects, most researchers recommend using trend lines based on growth increments over a period of a year, or multiples thereof (van Dam, 1999).

There is a general tendency in nearly all of the linear growth rate studies for sample sizes of immature turtles to decline as body sizes increase: for nearly all of the studies, some of the larger size classes are simply not represented (e.g., Bahamas, Cuba, Puerto Rico – Mona Cliff; Dominican Republic – all sites, US Virgin Islands, and Mexico). In some cases, it is thought that the larger immatures leave the study area and finish maturating in some other locations - as yet unknown (J. Horrocks, *in litt.*); for example, the largest size class at Barbados (70-79 cm) shows a sharp decline in growth rate, with an average that is less than the standard deviation. That is, some foraging sites for smaller sized hawksbills may be unsuitable for larger animals that are approaching maturity, perhaps because of energy or other nutritional requirements, refuge size, or other yet-to-be understood characteristics of developmental habitats.

The marked differences between linear growth rates reported from immature hawksbills at different study sites, particularly in the Caribbean emphasizes the need to understand environmental characteristics (particularly quality of habitat) and how they affect various biological characteristics of these turtles. Diez and van Dam (2002) speculate that differences in food abundance and quality are responsible for the different growth rates they found between immatures at Mono and Monito islands. In addition, other variables such as water temperature – which could affect metabolic activity – and population density are expected to influence growth rates of hawksbills, as well as other marine turtles. Carrillo *et al.*. (1998) demonstrated the effects of water temperature on growth rates if food was not limiting (in captive situations), and found effects of sea temperature on growth rates between different regions. The range of factors likely to effect growth throughout an individual's life time are enormous with any long-lived reptile and will likely defy accurate quantification. It is not necessary to understand the interaction of these variables in order to be able to derive predictions of mean ages to maturity at the population level of resolution. The density of hawksbills reported from different sites can vary greatly, from 3 to >200/km^2 (e.g., León and Diez, 1999; Prieto *et al.*., 2001). At Monito Island, where somatic growth rates are some of the highest in the region, the density of immature hawksbills in the "foraging aggregation" (i.e., animals of different genotypes from throughout the region) is one of the highest known (Diez and van Dam, 2002).

No evidence for density effects on somatic growth rates have been reported for hawksbills. To explore this question, studies at specific sites, monitoring density and habitat quality over periods of "years" (preferably at least for a decade), will be required for example the long-term work that has been done on foraging areas of immature green turtles in the Bahamas (Bjorndal *et al.*., 2000).

Table 5. Summary of information on growth rates of hawksbill turtles (*Eretmochelys imbricata*) in the wild. With the exception of data from Australia, all measurements are straight carapace, from anterior notch to posterior tip ("SCLnotch-tip"). All studies used mark-recapture time intervals of more than 1 year, except for those from Barbados, Cuba, and Dominican Republic, which measured growth rate for intervals of about 6 months or more, and extrapolated to yearly growth rates those values of < 12 months (see source for further details)

Study area	Size class: CL (cm)	Mean size of studied animals (cm)	Average growth rate (cm/yr) ± SD	Range of growth rates (cm/yr)	95% Confidence intervals*	Sample size: turtles; increments	Range of capture-recapture intervals	Notes	Source
Bahamas	30-35		15.7**			1			Bjorndal & Bolten, 1988
	40-45		5.9			1			
	60-65		2.4 ± 0.1			2			
	65-70		3.1			1			
West Coast bank reef, Barbados	20<29	28.9	4.13 ± 1.24	1.47-6.28	3.43-4.83	12	≥ 6 months	used average of initial and recapture size for grouping size class results	B. Krueger, unpubl
	30<39	36.85	3.48 ± 1.25	1.95-7.29	2.93-4.03	20			
	40<49	45.43	1.89 ± 1.45	-1.84-6.43	1.45-2.33	42			
	50<59	53.95	1.44 ± 0.82	0.00-3.15	1.04-1.84	16			
	60<69	64.45	1.53 ± 0.75	0.57-2.62	0.93-2.13	6			
	70<79	76.07	0.17 ± 0.55	-0.13-0.99	-0.37-0.71	4			
Doce Leguas + Isla de Pinos, Cuba	20<29	28.2	8.18 ± 0.79		7.63-8.73	8	≥ 6 months	used average of initial and recapture size for grouping size class results	Moncada & Nodarse unpubl.
	30<39	34.7	8.14 ± 2.4		7.16-9.12	23			
	40<49	44.7	6.89 ± 2.19		5.14-8.64	6			
	60<69	67.9	1.35 ± 0.54			2			
	70<79	78	1.24 ± 1.5			2			
	80<89 (nesting)	83.4	0.83 ± 0.98		0.15-1.51	8			
Mona Is.	20<29		2.63 ± 1.41	0.46 - 5.77	2.23-3.03	48; 68	> 12	compiled and	Diez & van

	30<39		3.07 ± 1.77	0.1 - 7.76	2.53-3.61	41; 101			
	40<49		2.9 ± 1.59	0.82 - 8.03	2.24-3.56	22; 74			
	50<59		2.22 ± 1.08	0.46 - 8.03	1.55-2.89	10; 38			
	60<69		0.74 ± 0.15	0.1 - 1.55	0.57-0.91	3; 5			
	70<79		0.25 ± 0.13	-0.59 - 1.42	0.16-0.34	8; 11			
	80<89		-0.29 ± 0.02	-		1; 1			
Mona Is. Cliff, Puerto Rico	20<29		2.65 ± 1.56	0.46 - 6.76	2.12-3.18	33; 52			
	30<39		3.17 ± 1.77	-0.49 - 5.38	2.54-3.79	31; 80			
	40<49		2.64 ± 1.43	0.71 - 7.14	1.80-3.49	11; 50			
	50<59		2.05 ± 0.63	1.06 - 5.01	1.34-2.76	3; 12			
	60<69		1.39 ± 0.17	0.88 - 1.9		1; 2			
Monito Is. cliff wall, Puerto Rico	20<29		6.48 ± 3.05	0.46 - 9.08	5.18-7.78	21; 22			
	30<39		6.47 ± 3.44	2.7 - 9.08	5.09-7.85	24; 40			
	40<49		5.35 ± 2.82	2.28 - 8.84	3.68-7.02	11; 29			
	50<59		4.19 ± 2.1	1.36 - 6.27	2.89-5.49	10; 25			
	60<69		3.91 ± 1.53	1.81 - 6.22	2.69-5.13	6; 12			
	70<79		2.69 ± 0.43	2.32 - 3.06		2; 2			
	80<89		1.33 ± 0.36	0.39 - 3.06	0.41 - 0.92	3; 3			
Lanza Zó, Dominican Republic	30<40		8.84 ± 1.25	7.2 - 10.5	7.74 – 9.94	5	> 6 months		León & Diez, 1999
Cabo Rojo, Muelle Oeste, Playa Oeste Dominican Republic	20<29		5.3 ± 1.45	3 - 7.2	4.45 – 6.15	11	> 6 months		
	30<39		4.04 ± 1.62	2.1 - 6.2	2.62 - 5.46	5			
St. Thomas, US Virgin Islands	30<34		6.6			1			Boulon, 1994
	35<39		3.8 ± 1.4			2			
	40<44		4 ± 2.4		1.28 - 6.72	3			
	45<49		2.2 ± 0.2			2			
	50<54		3.7 ± 1.0			2			
	55<60		1			1			
Ría Lagartos, Yucatán, Mexico	20<29		7.47 ± 2.2		6.55 - 8.39	22	300 to 1,466 days	used initial size for grouping size class results	Garduño, et al. unpubl.
	30<39		6.76 ± 1.8		6.22 - 7.30	42			
	40<49		6.55 ± 2.0		5.37 - 7.73	11			
	85<95 (nesting)		0.34 ± 0.26		0.17 - 0.51	9			

* Confidence intervals calculated for an ? ∂f 0.05 by ± 1.96 x [? /? (n)]

** not plotted in Figure 5 because the value, based on a sample of one, is an anomalous outlier

Age at maturity:

The only reliable methods to estimate age in these reptiles are through long-term mark and recapture or by analyzing cross-sections of dense bone (preferably the humerus) for annual growth rings, a technique known as “skeletochronology” (Bjorndal and Zug, 1995, see Chaloupka and Musick, 1997 for a review). In the case of hawksbills, which have relatively thick keratinous scutes, there have also been attempts to identify and decipher growth layers (e.g., Frazier, 1983; Ohtaishi, 1996; Tucker *et al.*, 2001) as well as periodic markings in surface patterns of the scutes (Kobayashi, 2000a, quoted in Kobayashi, 2000b). Age estimates derived from surface keratin have yet to be validated; and skeletochronology, is at present the most reliable method. However, this method requires hands-on intervention to live animals, and counts of annuli are always incomplete due to bone reabsorbtion and remodeling during normal processes of growth and metabolism. Therefore, estimations from skeletochronology are based on derivations of values that are only approximations.

Fundamental considerations in the estimation of age at maturity: The hawksbill life cycle is divided into three phases: pelagic, benthic-pre-reproductive, and reproductive (or adult). The pelagic phase of the life cycle extends from the time the newly hatched turtle crawls from its nesting beach into the sea, and swims off. It is now known that this pelagic phase may last for at least a decade in some populations of marine turtles (e.g., north Atlantic loggerheads) and this phase continues to present a source of major uncertainty in ecological studies of these animals. To get around this problem, investigators have focused on the last two phases, when the animals are found in benthic environments. For example, Boulon (1994) calculated that the average size when immatures are first seen in benthic environments in the US Virgin Islands is 21.4 cm straight carapace length ("SCL") and Diez and van Dam (1997) used the value of 20 cm SCL for the size when immatures first appeared in benthic environments in Puerto Rican waters. As a rule the pelagic phase of the life cycle from hatchling (about 4 cm SCL in the Caribbean) to the size when immatures are first seen in benthic environments, about 20 cm SCL for the Caribbean, has routinely been excluded from calculations.

Most data on growth rates are available from the intermediate phase, - the benthic, pre-reproductive animals. The final, reproductive phase would appear to be relatively straight forward, but there are a number of basic problems, for size at which sexual maturity is attained in hawksbills is little studied. Moreover, there is considerable variation in body size of adult animals, not only between populations, but also within populations. Hence, there is no simple means to derive a value that represents the minimum body size above which all animals are adults.

Use of relative age

On the basis of the average growth rates found in non-reproductive, foraging hawksbills in the US Virgin Islands, Boulon (1994) calculated that *after* reaching the average size when immatures are first seen in benthic environments (21.4 cm straight carapace length, "SCL") it could take 16.5 to 19.3 more years to reach the average size of nesting females.

Similarly, Diez and van Dam (1997; 2000; 2002) estimated the time that it would take turtles starting at 23 cm SCL (i.e., the beginning of the benthic phase) to reach 61 cm SCL (i.e., before reaching reproductive maturity), based on different growth rates from three different study sites. If the benthic animals lived *continually* at Mona coral reef, it would take 13.6 years to grow from 23 to 61 cm SCL; if they lived *continually* at Mona cliff walls it would take 16.1 years; and if they lived *continuously* at Monito Island it would take 4.8 years. Using a weighted mean derived from the data from all three study sites, Diez and van Dam (2002) estimated that it would take 10.4 years for a hawksbill to grow from 23 to 61 cm SCL. Further extrapolations to the size of mature individuals were not attempted by the authors for they considered that "… additional data for turtles outside of the size range covered [in our surveys] are needed to provide a complete age at maturity estimate for these turtles" (Diez and van Dam, 2000). As a point of comparison, mean size of nesting hawksbill females in Puerto Rico is 82.8 cms SCL (range of 70.8-92.3 cms SCL, Diez and van Dam, 2002; see Table 6)

Size of nesting females among Caribbean rookeries

There is considerable variation in body sizes of nesting hawksbills. Although most nesting hawksbills are at least 75 cm in carapace length, there are several reports from the Caribbean region of nesting females of about 60 cm, or less, in carapace length (Puerto Rico: Thurston and Wiewandt, 1976; Cuba: Moncada *et al.*., 1999;). However, in the Caribbean, it is rare to find nesting females less than 70 cm SCL, and the mean for all nesting populations is over 82 cm SCL (Table 6). On the other extreme, the largest mean sizes have been recorded in Yucatan, Mexico (e.g., Carrasco *et al.*., 1993; Gil *et al.*., 1993; Rodríguez *et al.*., 1993); recent information from Las Coloradas, Yucatan shows a modal value of 91 cm SCL (converted from the original in CCL) (Garduño, 1999). Interestingly, although the mean size of hawksbills from Yucatán is the largest (90 cm SCL), in the nearby state of Campeche, some of the smallest minimum sizes have been reported (70.9 cm SCL; Guzman, 2001).

The two extremes in mean sizes, 83 and 90 cm SCL, can be used to set limits in hypothetical models predicting the relationship between size and age in female hawksbills. Even though there are more sophisticated mathematical procedures (e.g., Chaloupka and Limpus, 1997), two simple approaches can be used to approximate the time taken to reach these two extreme mean sizes for nesting females, and thereby estimate age at maturity). When based on both fast and slow extremes in growth rates, these estimates provide a range of predicted values.

Table 6. Reported carapace lengths for nesting female hawksbills in the Caribbean

Rookery	*Min size*		*Range: Min-Max*		*Mode*		*Mean*		*S.D of mean SCL*	*N*	*Source*	*Original measurements*[1]
	CCL	SCL	CCL	SCL	CCL	SCL	CCL	SCL				
Doce Leguas, Cuba		64		64 - 93				83.5		45	Prieto *et al.*., 2001	SCL
Mona Island, Puerto Rico		70.8		70.8 - 92.3				82.8	5.6	47	Diez and van Dam in press	SCL
Costa Rica								83.8			Carr *et al.* (1966)	
Barbados	76	72.6	76 - 101	72.6 - 96.5			89.6	85.6	3.7	533	J Horrocks pers. com.	CCL
Jumby Bay, Antigua-“neophytes”[3]	76	72.6	76 - 96	72.6 - 91.7	88 - 90	84.1 - 86					J Richardson *et al.*., pers. com.	CCL
Jumby Bay, Antigua-“remigrants”[4]	84	80.2	84 - 98	84 - 89.8	92 – 94	87.9 - 89.8					J Richardson *et al.*., pers. com.	CCL
Guyana								85.5			Pritchard (1969)	
Campeche, Mexico		70.9	73.3 - 102.5	70.9 - 99.1			89.0 - 90.7	86 - 87.7			Guzman (2001)	CCLmin[2]
Las Coloradas, Mexico	76	72.6	76 - 114	72.6 - 109	95.5	91		90 - 91			M Garduno pers. com. and Garduño (1999)	CCL

[1]SCL and CCL represent “notch to tip” measurements, either straight or curved measured from the anterior point at midline (nuchal scute) to the posterior tip of the supracaudals. CCL were converted to SCL by $SCL = (CCL/1.0402)^{1/0.994}$ (formula from van Dam and Diez, 1998)

[2]CCLmin= minimum curved carapace length measured from the anterior point at midline (nuchal scute) to the posterior notch at midline between the supracaudals. Converted to SCL by SCL by $SCL = (CCL/1.0534)^{1/0.9986}$ (formula from van Dam and Diez, 1998)

[3]“Neophytes”= females observed nesting for the first time

[4]“Remigrants"= females that have been observed in previous nesting seasons found nesting in subsequent seasons

Integration of growth rate data

The first procedure followed the approach utilized by Diaz and van Dam (2002), involves “integrating” reported growth rates across incremental size classes (Figure 4) As mentioned by Diaz and van Dam (2002), caution should be exercised when interpreting these figures as the various errors are cumulative and result in widening confidence intervals that are not adequately represented in the graphs. While this procedure lacks in sophistication, it has an initial advantage in not assuming any growth model; hence, the derived curves reflect the available empirical growth rate (“GR”) data. By using mean, minimum and maximum values from the growth rate data set (Annex II) it is also possible to model extremes in the relative age vs. body size curves.

The results suggest that from the time turtles reach a body size of about 20 cm SCL, and began living in benthic sites, if they were to grow at the fast extreme in growth rates they could reach body sizes of 64, 83 and 90 cm SCL, in about 7, 17 and 25 years, respectively, (arrows in Figure 4). Using the slow extreme in growth rates to derive the same curves yields much higher estimates for the time required to grow from 20 cm SCL to the hypothetical adult sizes. However, the growth rate values are so slow in the higher size classes (>70 cm SCL) that the extrapolation yields estimates of several decades to reach adulthood. Clearly there is inadequate information on growth dynamics of larger immatures – particularly animals that are nearly adults, raising again the suggestions that large immature hawksbills may move into as-yet unstudied habitats for growth to maturity.

Use of the Von Bertalanffy growth function

The second approach (G. Webb and the Cuban Turtle Research Group, unpub. ms.) is based on a von Bertalanffy growth function derived from multiple regression between growth rate and mean SCL. This allowed an alternate set of growth curves predicting relative age at different body sizes (Figure 4). This technique "searches" for the best fit among the data points, deriving a mean curve that describes a declining growth rate as the animals grow larger and older. The von Bertalanffy model has been criticized when used for marine turtle growth analysis because it is questionable whether a monophasic function fits the mean growth profile of the complete post-natal developmental phase (Chaloupka and Musick, 1997),. However, Prieto *et al.*. (2001) also used a von Bertalanffy growth model for the Doce Leguas rookery and, assuming that it takes about 3-4 years for a hawksbill to reach 20 cm and recruit into benthic habitats, they estimated about 14 years for a female to grow to 80 cm SCL, and reach adulthood.

The curves from the von Bertalanffy model created in this summary are comparable to the results from the previous analysis which used the fast extreme in growth rates (Figure 4); beginning with the benthic phase at 20 cm SCL they yield predictions for reaching 64, 83, and 90 cm SCL sizes at about 7, 15, and 25 years, respectively.

It is important to point out that parameters that are used to derive the curves will result in major differences in the predicted values for age at maturity. For example, while it seems reasonable to use a 83.5 cm SCL to represent mature females in Cuba, this would not necessarily be an appropriate critical size for predicting age at maturity for other rookeries that have much larger means for nesting females. In the case of Las Coloradas, Mexico the mean in nesting females is about 7 cm larger so the estimated age maturity, with both the integrated curve and the von Bertalanffy FAST GR model would yield predictions a full 10 years older.

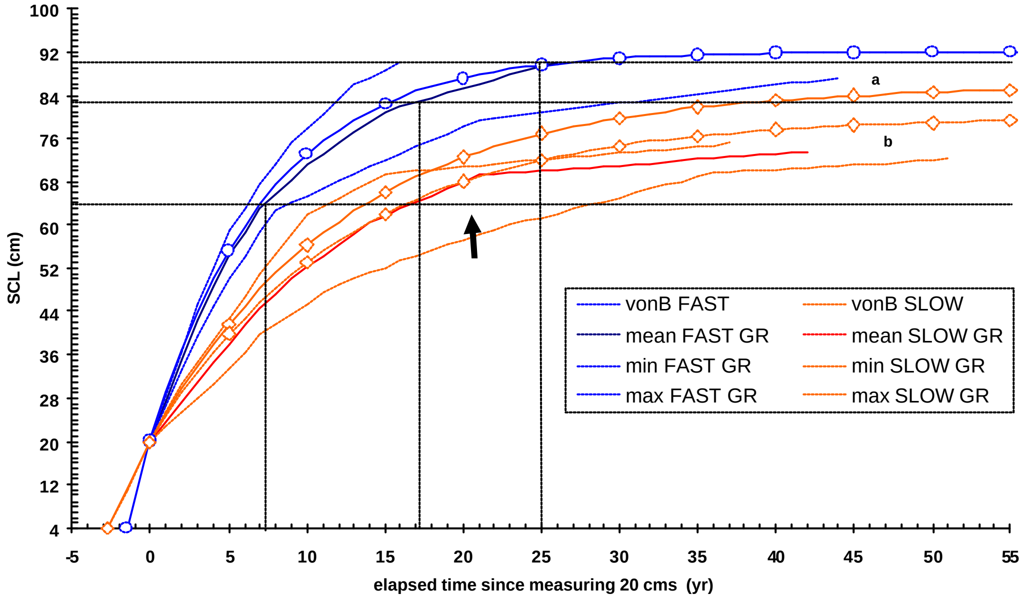


Figure 4. Straight-line carapace length (SCL) growth curves for hawksbill turtles, derived from data in Table 5. FAST growth curve was derived by integrating growth rate results from FAST growth habitats (Mexico, Cuba, Monito Island, Lanza Zó, and Bahamas; Table 5). SLOW growth curves, from data on growth in SLOW growth habitats (Mona Island, Barbados, USVI, and 3 sites in Dominican Republic; Table 5). "Mean", "Min", and "Max" curves for each of the FAST and SLOW growth curves correspond to the averaged values from the mean, minimum and maximal values of each set of habitats and size classes. "vonB FAST" and "vonB SLOW" correspond to the growth curves derived by von Bertalanffy modeling for the same two sets of growth data [the latter analysis kindly provided by G. Webb and the Cuban Turtle Group, unpub. ms]. Arrows indicate modeled relative age for critical SCL values of 64, 83 and 90 cm, roughly corresponding to smallest sized nesters in the Caribbean (in Cuba), and mean nesting female sizes in Doce Leguas and Las Coloradas rookeries, respectively. Arrow indicates a critical stage in SLOW GR studies, with large departures between modeled and observed growth rates (see text). Original Von Bertalanffy curves for SLOW GR results (b) which derived a maximal SCL of 80 cm, were also recalculated by forcing for an asymptotic SCL value of 92 cm SCL (a) for comparison. Arrow lines indicate approximate ages for 64, 83 and 90 cm SCL on the FAST GR curves.

Duration of the pelagic phase

Since there is no empirical information available on the duration of the stage between hatching and recruiting to benthic habitats, it is not possible to ascribe an informed value to this unknown. In the case of the loggerhead turtle in the North Atlantic this period may last 10 years or more (Zug *et al.*., 1995), providing time for the turtles to cross the North Atlantic, and return. It is likely that the pelagic phase of hawksbills depends on a much smaller area and takes much less time. Carr (1987) reported several pelagic records of juvenile hawksbills 5-12 cm SCL, in which the animals were associated with *Sargassum*; laboratory experiments demonstrate that neonate hawksbills are attracted to floating weed where they remain motionless for long periods (Mellgren *et al.*., 1994; Mellgren and Mann, 1996) and there is some evidence that some hatchlings may remain on reefs close to their natal beaches (Witzell and Banner, 1980; Witzell, 1983). Based on growth rates in demersal juvenile hawksbills, Musick and Limpus (1997) suggested a period of 1-3 years for the pelagic phase.

The von Bertalanffy SLOW and FAST functions can be used to extrapolate the time taken to reach the 20 cm SCL stage, by projecting the two curves back to 4 cm. While this procedure is not entirely acceptable, for it makes a number of untested assumptions about growth rates as well as the robustness of the curves, it is interesting to note that the rough predictions are between 1 and 3 years for the duration of the pelagic phase. This is consistent with estimates of growth rates based on neonate hawksbills held in captivity (Witzell, 1983), under conditions where growth would be expected to be maximized. More robust and informed estimations will require empirical data, possibly using appropriate ageing techniques such as have been recently reported for a better studied species such as the green turtle (Zug *et al*.., 2002).

Age at maturity for male hawksbills
The available growth studies all suffer from not separating the effects of sex on growth (precise sexing of immature animals can involve expensive laboratory work, the risks of intervention and trauma under inappropriate field conditions, and other drawbacks), and this makes it difficult to make anything more than general statements about growth and age in male hawksbills. If growth rates in Caribbean hawksbills are as different between sexes as shown in Australia, where males grow 25% slower (Chaloupka and Limpus, 1997), the growth rates and models for age estimates discussed in this summary would need to be revised drastically to apply to males.

If growth in males were to follows the same pattern as in females, and if they were to attain 100% sexual maturity at sizes as small as 68 cm SCL, they could become mature as early as about 7 years of age (Prieto *et al.*, 2001). Similar results would be obtainable using the current approach, with expected ages being considerably higher in SLOW GR sites and in populations where the mean size at maturity for males were to be shown to be higher. Growth rates for the sexes are a poorly studied subject which needs to be analyzed more closely.

Abundance and density:
There is very little information available estimating abundance and density of hawksbill turtles (Table 7). Recent, and historic, evidence from the Southern Great Barrier Reef (SGBR), Australia, indicates that the hawksbill is not as abundant as green or loggerhead turtles. Because this area has not been subjected to intensive exploitation, it was suggested that in some reef areas the species occurs naturally at low densities (Limpus, 1992).

Table 7. Summary of abundance and density values for hawksbill turtles; JNP/CR, DR = Jaragua National Park/Cabo Rojo, Dominican Republic.

Study area	Sighting rate (turtles/hr) average; range	Capture rate (turtles/hr)	Density (turtles/km^2)	Biomass (kg/km^2)	Source
Mona Island; Puerto Rico		0.48 - 2.38			Diez & van Dam, 1998
JNP/CR, DR: 11 sites	1.62; 0.08 - 3.43	0.00 - 3.43			León & Diez, 1999
JNP/CR, DR: 5 best sites:	1.85; 1.01 - 3.28	0.86 - 3.43	35.8 – 568.1	35.8 - 568.1	León & Diez, 1999

* values calculated from a mark and recapture study.

Hawksbill turtles are especially common in shallow coastal waters, with hard bottom communities such as scleractinian coral reefs, but quantitative studies, based on systematic methods, are rare. Sighting frequencies in 11 snorkeling sites at Jaragua National Park/Cabo Rojo, Dominican Republic, ranged from 0.08 to 3.43 turtles/hr, averaging 1.62 turtles/hr. Densities at 5 select sites ranged from 5.6 to 96.8 turtles/km^2, with biomass estimates ranging from 35.8 to 568.1 kg/km^2 (León and Diez, 1999). It is important to appreciate that these values are based on selected areas of high concentration of hawksbill juveniles, varying in surface area from 0.03 to 4.02 km^2 and no deeper than 15 m. The overall density values for the entire area of the park will be markedly lower.

STATUS OF HAWKSBILL POPULATIONS

The status of the hawksbill turtle (*Eretmochelys imbricata*) in the Caribbean and globally has been the subject of numerous reports, including a global review that was undertaken by Groombridge and Luxmoore (1989) for the CITES Secretariat. In 1999 the journal *Chelonian Conservation and Biology* dedicated an entire volume to an in-depth review of this species, including the "Status Justification for Listing the Hawksbill Turtle (*Eretmochelys imbricata*) (Meylan and Donnelly, 1999) and "Status of the Hawksbill Turtle (*Eretmochelys imbricata*) in the Caribbean region" (Meylan, 1999b).

Distribution

Hawksbill turtles are circumtropically distributed in coastal waters; they are found in the waters and on the beaches of 82 geopolitical units and may occur in 26 others. Nesting occurs on beaches in at least 60 countries, although much of this nesting occurs at low density (Groombridge and Luxmoore, 1989). No major rookeries have been documented in the eastern Atlantic Ocean; along the Pacific coast of North, Central, or South America; or in the Central Pacific (Groombridge and Luxmoore, 1989; Eckert, 1993; Limpus, 1995).

Hawksbills spend their first years of life in open ocean at the surface of the sea. Larger juveniles and adults are closely associated with coral reefs, but they also forage on other hard bottom habitats throughout the tropics and, to a lesser extent, the subtropics. Hawksbills nest on insular and mainland sandy beaches.

Current Status Designations

IUCN Red List of Threatened Species

Based on the situation as of 1996 and using the 1994 Criteria and Categories, the hawksbill is listed as Critically Endangered (IUCN, 2001). An update on the Red List designation based on most recent population status information and using the revised Categories and Criteria has not been completed.

CITES

The hawksbill has been afforded protection under CITES since 1975 when the treaty came into force. At that time, the Atlantic population was included in Appendix I and the Pacific population was included in Appendix II. In 1977 the Pacific population was moved to Appendix I. Legal CITES trade did not cease until the end of 1992, when Japan adopted a zero import quota on its reservation on *E. imbricata*.

Other Multilateral Agreements

The hawksbill is listed in Appendix I and Appendix II of the Convention on Migratory Species (CMS). In 1991, the Parties to the Cartagena Convention voted unanimously to include *E. imbricata* in Appendix II of the SPAW Protocol (Specially Protected Areas and Wildlife) of the Cartagena Convention, conferring full protection to the species. All sea turtle species in the Western Hemisphere are afforded protection in the signatory countries under the Inter American Convention for the Protection and Conservation of Sea Turtles, which came into force in 2001.

Estimating Population Size

Sea turtles are difficult to census because they are highly mobile. For reasons of accessibility, the most commonly used method of monitoring population trends is to count the number of females arriving annually at nesting beaches (Meylan, 1982). Population estimation is complicated by the fact that females nest several times within a breeding season, they typically follow a non-annual breeding schedule (intervals of which may vary in length), and they may be reproductively active for decades (Carr *et al*.., 1978; Fitzsimmons *et al*.., 1995; Mortimer and Bresson, 1999). Long-term monitoring is thus essential to document true population change. Also it is essential to realise that adult females only represent a small part of the entire population and that trends in this part of the population not necessarily reflect trends in the male and immature part of the population. Limited access to reproductive males and to all nonreproductive segments of the population makes it difficult to estimate total population size.

Annual numbers of nests is preferred to the number of individual turtles as a measure of population size because many projects do not involve tagging turtles (only tracks), so multiple nests by the same individual cannot be distinguished. Use of annual totals also avoids the need for animals to be marked for recognition in future nesting seasons (remigrations) and makes it unnecessary to factor in geographic differences in remigration-interval frequencies. The numbers of nests constructed annually can be related to the number of female turtles nesting annually by dividing by the average number of nests per female (Richardson *et al.*., 1989; Guzmán *et al.*., 1995; Hillis, 1995). For the purposes of this review, a range of 3-5 nests per nesting year per female has been used. The most common remigration intervals for female hawksbills in the Caribbean are two and three years (Corliss *et al.*., 1990; Hillis, 1994a, 1994b).The number of nesting females could be related to total population size (though not precisely) if appropriate data for the population were known (sex ratio, population structure). This is rarely possible because of lack of sufficient information.

Long generation times in marine turtles also have implications for population trend analysis (Congdon *et al.*., 1993). Generations are calculated as the age at sexual maturity plus half of reproductive longevity (Pianka, 1974). Estimates of age-at-maturity for wild marine turtles are high for hawksbills, ranging from about 20 to 40 years (Boulon, 1983, 1994; Limpus, 1992, pers.comm.; Mortimer, 1998; C. Diez and R. van Dam, pers.comm.). Average generation time in hawksbills globally has been estimated to be 35 years, based on growth and reproductive longevity data from around the world (Meylan and Donnelly, 1999). Data collection has been restricted by the fact that scientific monitoring of marine turtle populations on nesting beaches only began in the mid-1950s, and relatively few projects have focused on the hawksbill.

One result of long generation times is that nesting beach surveys more accurately measure the reproductive success of nesting females and the survival of their offspring than the status of the total population. Nesting beach surveys fail to detect changes in the juvenile and subadult turtle populations that result when overharvest of eggs or females at the nesting beach interferes with the production of new offspring. When such overharvest is intense, an observation of the decline in numbers of nesting females will be delayed until their offspring have passed through the juvenile and subadult age classes (Bjorndal *et al.*., 1985; Mortimer, 1995) and a new cohort of females starts nesting.

In 1999, Meylan (1999b) estimated that a maximum of 5000 hawksbills nest annually in the Caribbean region, excluding Guyana, French Guiana, Suriname, and Brazil. A maximum of 600 hawksbills are estimated to nest in these four countries, based on the following estimates: 1-5 nests/yr in French Guiana (J. Fretey, 1987, pers. comm.), 30 nests/yr in Suriname (Reichart and Fretey, 1993), and 1200-1500 nests/yr in Brazil (M. Marcovaldi, pers. comm.). Nesting by hawksbills occurs at low densities in Guyana; a countrywide estimate is not available.

Updated population assessments including, where available, nest totals are provided in Annex III and data for seven regularly monitored hawksbill nesting sites in the Caribbean are presented in Table 8. The recent nesting data for the seven systematically monitored sites in Table 8, along with historical nesting data (1950's onwards) and several other measures of trends in abundance, are graphed in Figures 5 and 6, in order to provide a longer-term perspective of population changes. In order to use similar units to compare across data from different sources, the nest counts from the recent nesting data presented in Table 8 have been converted to number of nesting females per year by dividing by three (Meylan and Donnelly, 1999).

Four populations (Yucatan, Mona, Doce Leguas Cay, and Barbados) show an increasing trend in the number of nests in recent years, with the largest increase (mean % change per year of 35.1%), having occurred in Barbados, which has been regularly monitored for the last five years. Mexico, harbouring by far the largest hawksbill nesting population in the Caribbean, has experienced a mean annual increase of 18.2% over the last 12 years. Buck Island (USVI) and Jumby Bay (Antigua), both with 15 years of monitoring, show a stable number of nests. Trend analysis at Tortuguero is a bit more complicated. Using the data set for 1972-2001, the mean % change per year is not significantly different from 0, but if one examines the trend from 1990-2001, it is increasing by 29.6% ($r^2 = 0.42$, c.i.$_{95\%}$ =+4.6% - +60.7%). For all sites in the table except the Yucatan, 2001 was a record year for number of nests. The Yucatan nesting beaches were down from a record high of 6,395 nests in 1999 to 3,969 nests in 2001.

Several patterns are apparent in Figures 5 and 6. First, there are several indicators of increasing abundance of hawksbills in the region in recent years, such as the number of nests documented annually at four nesting beaches (including the very large rookery in the Yucatan), plus catch-per-unit-effort in the Cuban hawksbill fishery. Second, increases in numbers of hawksbill nests from 1987 onwards at the four sites in Table 8 occurred against a background of little or no reported international trade in tortoiseshell. Third, trends in hawksbill abundance over the last half-century (the maximum period for which regular monitoring data exist) seem to be strongly decreasing, e.g., Tortuguero (Costa Rica) -- 82% decline from 1956-20002000 (but rising again with + 5.1% per year since 1985); Nicaragua – 92% decline from 1970-1996; and Chiriqui Beach (Panama) – 98% decline from 1950 – 1990. Although there are few quantitative historical data sets available, the pattern of decline at these three localities is consistent with the qualitative data available for the Caribbean (Meylan, 1999b; Meylan and Donnelly, 1999) and with other evidence of the assumed previous abundance of hawksbills in the region, such as the volume of trade in shell. Exports to Japan from Latin America and the Caribbean during 1970-1986 represented 244,730 turtles (at 1.34 kg shell/turtle). Fourth, declines in the abundance of hawksbills over the last half-century closely track the decline in the number of hawksbills represented in trade between Latin America/ Caribbean and Japan from 1970-86.

The nesting beaches identified in Table 8 show the potential for recovery of hawksbill populations under the scenario of nest protection and a near cessation of international trade. In an extensive review of the histories of various marine ecosystems, Jackson *et al.*. (2001) conclude that the magnitude of recovery potential of marine resources is extraordinary. They also suggest that ecosystem restoration efforts should be guided by a historical perspective in order to reach their full potential.

There are encouraging signs of increasing numbers of nests at a small number of well-protected or remote nesting sites. Significantly, one of these, in the Yucatan, is by far the largest population in the entire region, and it is likely to contribute heavily to population recovery in those areas where the various life history stages of this population reside. Similar contributions in their respective distribution areas will be expected from the other populations where recent increases have been detected. However, the hawksbill's complex nesting distribution, which includes both sites of concentrated and dispersed nesting, leaves many small populations (including some that were large historically) unmonitored and unprotected. There is no easy way to take these populations into consideration when evaluating the status of the species in the region. These populations are highly vulnerable, and their loss would spell the loss of genetic diversity and the loss of certain ecosystem functions in the areas where those hawksbill populations reside. For example, there is good evidence that hawksbill predation on sponges may be an important factor regulating sponge-coral interactions (Hill, 1998) and is thus important to maintaining healthy coral reefs.

Only enhanced monitoring and research of hawksbills throughout the Caribbean can reliably provide population data that will guide recovery efforts. To address the need for better population status data, approximately 30 nesting beaches and 30 foraging areas were selected as candidates to serve as indices of the hawksbill's status at the Hawksbill Protocol Meeting in Miami, in February 2002. Using standardized methodologies, the network of researchers involved in monitoring these areas will hopefully provide the needed data.

Additional information (both quantitative and qualitative) on important areas in the Caribbean is given below.

Antigua. The nesting population at Jumby Bay, Antigua, appears to be stationary (Meylan, 1999b; Richardson *et al.*., 1999) with a peak of 139 nests in 1991, and an estimated population of 78 adult females. (Richardson *et al.*., 1999) (see Annex II). Surveillance of the nesting beach at Jumby Bay is very thorough. Nesting females and nests are currently well protected because the beach belongs to a private resort that is conservation-oriented. No other sites of concentrated nesting in Antigua are known. Additional tourism development at Jumby Bay and increased human presence are of concern.

Barbados. The total number of hawksbill nests recorded in Barbados increased from 328 in 1997 to 807 in 2000 and to 1179 in 2001 (Table 8, Fig. 6). This includes nesting activity on approximately 10 km of beaches and is estimated to represent 80% of the total hawksbill nesting activity in Barbados (J. Horrocks, pers. comm.). In 2000, 103 nesting females were tagged. Barbados has recorded a steady increase in nests and numbers of female hawksbills tagged since 1997, and researchers there are increasingly confident that the population is in the early stages of recovery (J. Horrocks, pers. comm.). Although, numbers of hawksbill nests have been increasing researchers in Barbados consider it too early to say that the population itself is increasing (J. Horrocks, in litt.)

Colombia. In 1969, fishermen interviewed by the investigators reported catching up to 100 hawksbills per day previously in their lifetimes (exact time frame not given). As part of the investsigation, four local divers working for seven hours captured one hawksbill at Quitasueño bank (capture rate - 1 hawksbill per 28 man-hours); three worked eight hours to catch six hawksbills on Serrana Bank (1 hawksbill - 4 man-hours) (Ben-Tuvia and Rios, 1970).

In 1980 the findings of interviews and ground surveys conducted in the San Andrés Archipelago (specifically the islands of San Andrés and Providencia and on the four atolls of East Southeast Cays, Albuquerque Cays, Roncador Bank, and Serrana Bank) reported that hawksbills were depleted there (Carr *et al.*., 1982). Combined takes of hawksbills and loggerheads had declined from 100 turtles per boat per season to 25 (75% decline), according to interview data. In addition, Carr reported that divers spear-fishing for snapper and grouper and snaring lobsters were also taking hawksbills incidentally and would continue to do so even when the hawksbills became very scarce (Carr *et al.*., 1982). This phenomenon pertains elsewhere around the Caribbean and throughout the tropics because of the overlapping of habitats among these valuable, reef-dwelling species and the relative ease with which hawksbills are captured (Carr and Meylan, 1980).

Cordoba (1997) surveyed for hawksbills in the San Andrés Archipelago in 1996, including San Andrés, Providencia, Catalina, Bolivar, Albuquerque, Roncador, Serrana, and Serranilla. During beach surveys conducted from mid-April to the end of November (encompassing the nesting season), a total of 21 hawksbill nests (representing 4-7 females) were recorded (Cordoba, 1997; Cordoba *et al.*., 1998).

Costa Rica. Tortuguero National Park includes a 35-km nesting beach which has been monitored since 1955, primarily for the green turtle (Carr and Giovannoli, 1957), although nesting events by all species encountered are recorded. Carr and Stancyk (1975) compared the number of hawksbills encountered per unit of patrol effort for two four-year periods. Encounters decreased substantially from 2.3 hawksbills per unit of patrol effort in 1956-59 to 0.60 in 1970-73. The equivalent value for 1988-91 was calculated by Bjorndal *et al.*. (1993) to be 0.35 hawksbills, indicating a decline of 85% from 1956-59 levels (less than one generation time). A comparison of the number of hawksbill encounters per unit effort in 4 four-year periods from 1956-1959 to 1997-2000 shows a mean annual decline of 3.9% and a total population decline during this period of 82% (Tröeng, 2002; Tröeng, in press). However, the number of encounters per unit effort increased slightly between the two most recent 4-year periods (1988-1991 and 1997-2000) (Figs. 5 and 6). Tröeng (2002) reports that the recent (1985-2000) trend shows an increase of 5.1% per year or 111% over the 15-year period. He notes, however, that patrol effort may have varied between years, and if effort varied greatly among years (in terms of number of months patrolled) the trend estimate may be unreliable.

Mean carapace length of nesting hawksbills at Tortuguero was found to have decreased significantly from 1955 to 1977 (p=0.0005), indicating population instability (Bjorndal *et al.*., 1985).

From 1980 to 2000, a maximum of 13 hawksbill nests were recorded annually at Tortuguero on the 8 km of consistently patrolled beach (see Annex III). Eighteen nests were recorded on the 8 km of regularly monitored beach at Tortuguero in 2001 (Table 8, Fig. 6). This represents only a sample of the total number of nests on the 36-km nesting beach. Newly established surveys in southern Costa Rica near Cahuita documented a total of 17 hawksbill nests in 2000 (through July) and 14 nests in 2001 at Gandoca, near the border between Costa Rica and Panama (D. Chacon, pers. comm.).

Cuba. On the basis of survey data, Moncada *et al.*. (1999) suggested that although Cuba has extensive shoreline that appears suitable for nesting by hawksbills, most nesting activity is confined to small beaches on offshore islands. The most important nesting area identified to date is the Doce Leguas Keys which lie 60 km off the southern coast (Camagüey Province) (Moncada *et al.*., 1999). The total number of nests documented annually in the Doce Leguas Keys during the 1994-1995 to 1997-1998 seasons has ranged from 105 to 251 nests (Moncada *et al.*.,1999). The authors cautioned that these totals did not reflect all nesting activity and that the true total is undoubtedly higher. However, they also reported that nesting activity by hawksbills appeared to be reduced in Doce Leguas in 1997-1998 compared to previous seasons, and attributed the decrease to human disturbance and beach erosion. In 1997/1998, a total of 403 hawksbill nests, representing 101 females, were found in "spot checks" throughout the southeastern zone of Cuba (including Doce Leguas Keys). Nine index beaches, representing 3.2% of total available nesting area, have been consistently monitored since 1997 in Doce Leguas Cays, the most important nesting area in Cuba (Table 8, Fig. 6). A total of 72 nests were recorded on these nine beaches during 2001. Search effort has averaged 45.9 +/- 5.1 (SE) days per nesting season for 1997-2001, with nest totals during this 5-year period showing a mean annual increase of 20.2% (Cuban Turtle Group, in litt. to A. Abreu, 6 February 2002). An estimate of the total number of nests in Cuba, based on extrapolations from these index beach totals to the entire nesting season and all nesting beaches in the country is 2250 (range 2000-2500) (Cuban Turtle Group, in litt. to A. Abreu, 8 February 2002).

The importance of Cuban feeding grounds for hawksbills has long been established. Doce Leguas Keys (formerly known as the Archipélago Jardines de la Reina), off the south coast of Cuba, was known as an early center for tortoiseshell trade and is believed to be where Cayman fishermen used to net hawksbills (Parsons, 1972). Genetic research has revealed that feeding ground populations are composed of an estimated 65% Cuban-born turtles, with the remainder from Belize, Costa Rica, Mexico, Puerto Rico, the U.S. Virgin Islands, and Antigua (Bass, 1999; Caribbean Conservation

Corporation, unpublished data). An organized hawksbill fishery has existed in Cuba since 1968. Between 1968 and 1990, annual harvest for shell and local meat consumption averaged 4744 animals per year (Carrillo *et al.*., 1999). After 1990, Cuba voluntarily phased down the harvest quota to 500 animals. J. Frazier (in litt.) noted that increased records of hawksbills nesting in Mexico have coincided with the decreased harvest in adjacent Cuban waters. Although the decreased Cuban harvest may be a possible factor, increased recruitment into the reproductive population from hatchlings produced in Mexico, and higher survival rates of juveniles, subadults and adults due to local conservation measures are considered to be the primary causes of increased nesting in Mexico (Garduño *et al.*. (1999).

Guatemala. Surveys conducted for 12 weeks in 2000 on 10 km on nesting beach on the Manabique Peninsula near Jaloa documented 34 nests; in 2001, surveys were extended to 12 km and 14 weeks, and 22 nests were recorded (W. Katz, pers. comm.). No historical data or previous estimates are available for comparison.

Honduras. Nesting beaches were monitored within the Archipelago of Cayos Cochinos in 1999 and 2000, with 34 and 10 hawksbill nests recorded, respectively (Aronne, 1999, 2000).

Jamaica. An estimated 200 – 275 females nest in Jamaica based on beach surveys from 1991-1996 (R. Kerr, pers. comm.). Jamaica has lost more than 90% of its coral reef habitat since 1980 (R. Kerr, in litt). Nesting beaches are threatened by extensive tourism development with its attendant problems.

Mexico. Mexico has a relatively large and increasing number of nests (Guzmán *et al.*., 1995; Garduño *et al.*., 1999). In 1996, a total of 4522 nests were recorded in the states of Campeche, Yucatán, and Quintana Roo, representing a seven-fold increase in survey area and a 56-fold increment in nests compared to the number of nests protected in 1977 (Garduño *et al.*., 1999). Garduño *et al.*. (1999) considered the increased nesting levels during the period 1977-1992 to be best explained by increases in monitoring efforts, but attributed increases from 1993 to 1996, when beach coverage was maximized, to true population change. Guzmán *et al.*. (1995) concluded that the increased number of nests recorded in the state of Campeche in recent years was a sign of gradual, effective recovery and noted that the increase in Campeche had come after 17 years of protection of the beaches. Annual nest totals for 1997-2000 are presented in Annex II. In 2000, 5595 nests were recorded in the Yucatán (V. Guzman, M. Garduño, K. López, and M. Medina, pers. comm.), representing 1119 – 1865 females (assuming an average of 3 – 5 nests/female/season, Richardson *et al.*., 1989; Hillis, 1995; and Guzmán, *et al.*., 1995) but not every beach that previously had been monitored was covered in this year.

Netherlands Antilles. Very low levels of hawksbill nesting (4 confirmed nests in 1993) were reported for beaches along the northeast coast of Curaçao (Debrot and Pors, 1995). Hawksbill nesting had not been previously documented on the island in recent times.

Nicaragua. Nietschmann (1981) estimated that 1000-1200 hawksbills were harvested annually along Nicaragua's east coast in the late 1960s and early 1970s. Lagueux (1998) recorded minimum landings of 86, 109, and 53 hawksbills in 1994, 1995, and 1996 (avg.= 83), respectively, at eight of the principal turtling communities and Caribbean coastal commercial centers from Sandy Bay in the north to Set Net in the south (just north of Bluefields). This coverage represents the majority of the area where harvesting occurs; it does not include landings by Rama Indians in the southern part of the country. Lagueux's recorded minimum landings represent a decline in capture rate of 92% in 28 years (less than one generation time for the hawksbill turtle).

Lagueux (1998) also compared total landings of hawksbills in the community of Tasbapaune during the same six-month period in 1968 and 1971 (Nietschmann, 1972, 1973) with those from the same six-month period in 1995, 1996, and 1997. The average number for 1968 and 1971 was 67; for 1995, 1996, and 1997, it was 14 hawksbills per year (a decline of 79%). Lagueux (1998) attributed the change to a decline in the hawksbill population rather than to a decline in the demand for hawksbill shell. She reported that the tortoiseshell market in Nicaragua remained active, with demand for shell created by cottage-based industries and retail jewelry stores.

Surveys in the Pearl Cays were conducted weekly during the 1999 nesting season on 11 cays, and daily during the 2000 and 2001 nesting seasons on 11 and 10 cays, respectively. Nest totals for these three years were 99, 152 and 156 (C. Lagueux and C. Campbell, pers. comm.). Nest poaching was estimated to be 97% in 1999, and was reduced to 30.3% and 31.5% in 2000 and 2001, respectively, by conservation efforts. Continuing threats include taking of nesting females and of all sizes of hawksbills on nearby foraging grounds, and habitat destruction or alteration.

Nest surveys were conducted in 2000 at El Cocal, along the mainland coast of southern Nicaragua. The surveys were done on 27 km of beach once every three weeks between April and October. A total of 75 hawksbill nests were recorded, 73.3% of which were poached (C. Lagueux and Campbell, pers. comm.). El Cocal and the Pearl Cays are considered to be the best remaining hawksbill nesting areas on the Caribbean coast of Nicaragua (C. Lagueux, pers. comm.).

Panama. Chiriqui Beach, Bocas del Toro Province, Panama is described (Carr, 1956) as the most important hawksbill nesting beach in the Caribbean. Records of the beach date back to at least the early 1800s, when Roberts (1827) mentioned its importance in his account of bartering for tortoiseshell in the region in 1815. The yield of hawksbills from this 29-km beach has been sufficiently important to the local economy during the 20th century that the beach was divided into approximately one-mile sections and leased out by the government. *Veladores* or “stayers awake” paid a head tax for the rights to all female hawksbills nesting on their section of the beach. Former *veladores* interviewed in the 1980s independently reported capturing as many as 35 to 50 hawksbills on their one-mile section per night in the early 1950s (Meylan and Meylan, unpublished data). Assuming the nesting density was equal throughout the beach, this would represent a maximum of 900 females nesting on a single night. One section called Satu produced a total of 200-300 hawksbills in 1942. These same *veladores* estimated that one could catch only between 1-5 hawksbills per night in 1980 (a 90% decline from the early 1950s). The government’s leasing system was no longer in effect in 1980, although the Ngobe Indians still had a system of allocating rights to hawksbills nesting on Chiriquí Beach. Ground surveys of the entire beach in 1980 and 1981 during the nesting season revealed 17 and 13 tracks, respectively; the tracks were of various ages and included both successful and unsuccessful nesting attempts (Carr *et al.*., 1982). Assuming a maximum of 17 nests for the entire beach, this would represent a decline of 98% from 1950 levels. Aerial surveys of the beach from 1979 to 1981 also did not reveal any significant nesting. A ground survey of the entire beach during the 1990 nesting season documented one hawksbill nest and two non-nesting emergences (Meylan and Meylan, unpublished data). Six groups of Ngobe Indians were encountered on the beach looking for hawksbills during the night of the survey. This nesting aggregation can be considered severely depleted.

U.S. Mainland, Puerto Rico, and U.S. Virgin Islands. In a 1995 review of the status of hawksbills in U.S. jurisdictional waters within the Atlantic Ocean and Caribbean Sea (Florida, Puerto Rico, U.S. Virgin Islands), Eckert (1995) estimated that the area hosted a minimum of 650 nests per annum or approximately 130-216 nesting females. Meylan (1999b) increased this estimate to 1050 nests (650 in Puerto Rico, 400 in US Virgin Islands) due to increased nesting on Mona Island (Diez *et* *al.*., 1998; C. Diez and R. van Dam, pers. comm.) and data from new monitoring efforts on mainland Puerto Rico (K. Hall, in litt.; C. Diez, in litt.).

Mainland - Only 1-4 nests have been recorded annually in Florida from 1979 – 2000 (Meylan *et al.*., 1995, Florida Statewide Nesting Beach Survey database).

Puerto Rico - The hawksbill nesting population at Mona Island, Puerto Rico, is considered to be increasing, with a record number of nests (541, representing 108 to 180 females) documented in 2000 (C. Diez and R. van Dam, pers. comm.). Diez and Van Dam (in press) consider Mona Island to be the largest rookery for hawksbill turtles in the Caribbean Basin. A total of 549 nests were recorded on Mona Island in 2001 during the main portion of the nesting season (Table 8, Fig. 6). Additional nest totals for elsewhere in Puerto Rico in 2000 were as follows: Caja-de-Muerto (58), Vieques (50), Humacao (145), and Culebra (20) (C. Diez, pers. comm.).

US Virgin Islands - The nesting population at Buck Island Reef National Monument, U.S. Virgin Islands, appears to be stationary with a peak year of 135 nests in 1995.

Venezuela –The Peninsula of Paria in the state of Sucre is considered to be the most important hawksbill nesting area on the mainland (Buitrago and Guada, 2001). Partial censuses documented 33 hawksbill nests in 1997, and 65 nests in 1998 (Guada, 2000). Los Roques Archipelago is an important offshore nesting area, with 31 nests per year during 1979-1983 and 32 confirmed nests in 1998 (Guada, 2000; Mata *et al.*., in press). These nest counts for both localities are considered to be underestimates of the total. Although data are limited, Buitrago and Guada (2001) estimate approximately 120-150 nests per year in Venezuela.

Table 8 - Trends in number of nests of hawksbill turtles (*Eretmochelys imbricata*) recorded annually at seven regularly monitored beaches in the Caribbean, mean % change per year, and possible feeding grounds used by adult females from that beach inferred from tag returns and satellite tracking experiments. For these recent time series (5 to 15 years) presented in Table 2, the mean percent change in nest totals per year has been calculated for each nesting area. Trends were estimated as the coefficient *r* (also known as the intrinsic rate of change) from the exponential regression of annual number of nests vs. year (annual number of nests = constant x ($e^{r\ year}$)). Mean rate of change per year (as percentage) was converted from this coefficient by the expression: ((e^r) - 1) x 100. It is important to point out that the trend indicated by this measure applies to changes in number of nest laid per year, and not to a measure of population increase as data covers a period of time much less than a single generation.

	Yucatan Peninsula MEXICO	**Buck Island USVI**	**Jumby Bay ANTIGUA**	**Isla Mona PUERTO RICO**	**Doce Leguas Cays CUBA**	**Tortuguero COSTA RICA**	**BARBADOS**
1987		73	103			10	
1988		126	154			12	
1989		116	129	126		6	
1990	826	79	77	196		3	
1991	1,053	119	139	142*		1	
1992	1,282	88	114	142*		4	
1993	1,891	101	107			0	
1994	2,563	118	109	308		4	
1995	3,690	135	126	157*		2	
1996	4,522	114	82	354		12	
1997	2,671	85	94	475	34	10	328
1998	4,701	121	117	503	32	9	515
1999	6,395	94	120	511	70	12	717
2000	5,746*	65	113	541	45	9	807
2001	3,969	143	159	549	72	18	1,179
Mean % change per year	+18.2%	stable	stable	+12.6%	+20.2%	stable (1972-2001)	+35.1%
Upper c.i.	25.5%	2.7%	2.1%	15.7%	61.2%	2.5%	48.9%
Lower c.i.	11.3%	-5.0%	-3.5%	9.5%	-10.3%	-6.5%	22.5%
R^2	0.79	0.04	0.03	0.94	0.57	0.03	0.97
Tag return sites and end points of satellite tracks for adult females	Dominican Republic, Mexico	British Virgin Islands, Cuba, Nicaragua Puerto Rico	Antigua, Dominica, Netherlands Antilles, St. Kitts & Nevis	Nicaragua, Puerto Rico, St. Bartholemy, Turks & Caicos, offshore Honduras/ Nicaragua	Cuba, Honduras	Honduras, Nicaragua,	Dominica, Grenada, Trinidad, Venezuela

* Partial counts

Sources for nest totals:

- **Yucatán Península, Mexico**: Garduño-Andrade *et al.*., 1999, V. Guzmán, M. Garduño, K. López González, M.Medina, pers.comm.;
- **Buck Island Reef National Monument, St. Croix, US Virgin Islands**: Z. Starr Hillis and B.Phillips, pers. comm.;
- **Jumby Bay, Antigua**: Hoyle and Richardson, 1993; J. Richardson, pers. comm.; R. Kerr, pers. comm.;
- **Mona Island, Puerto Rico**: Diez and Van Dam, in press; C. Diez, pers. comm.;
- **Doce Leguas Cays, Cuba:** F. Moncada, in litt. to A. Abreu, 6 Feb. 2002. Doce Leguas data are for nine index beaches only;
- **Tortuguero, Costa Rica**: Tröeng, 2002; Caribbean Conservation Corporation, unpublished data. Tortuguero data are for northern 8 km of 35-km beach.
- **Barbados**: Horrocks and Kreuger, unpub. data. Sources for tag return and satellite data: B. Schroeder & Balazs, pers. comm.; Meylan, 1999b, Horrocks *et al.*., 2001; Prieto *et al.*., 2001; and M. Garduño, pers. comm. to A. Abreu).

Explanatory notes for figures 5 and 6

Data for Tortuguero are presented using two different measures, number of hawksbill encounters per unit of patrol effort for four 4-year periods between 1956 and 2000 (Tröeng, 2002, in press) (Figure A1) and numbers of nests per year (1972 – 2001) (Figures 5 and 6).

Trends in exports of tortoiseshell to Japan from Latin America and the Caribbean from 1970-86 are measured in terms of hawksbill equivalents (1.34 kg/turtle) (Milliken & Tokunaga, 1987). The graph also shows the number of hawksbill equivalents represented by imports of tortoiseshell to Japan from Cuba and Haiti from 1987-1992, combined with tortoiseshell harvested (but not exported) in Cuba from 1993-2000 (Ottenwalder, 1996; Prieto et al., 2001; TRAFFIC, 2001) (Figures 5 and 6).

Estimates of numbers of nesting females per night at Chiriqui Beach, Panama, are based on interviews (1950's and 1980/1981) and ground surveys (1980/1981 and 1990) (Meylan & Donnelly, 1999). Data on annual captures of hawksbills along the east coast of Nicaragua in 1970 are from Nietschmann (1981), and in 1994, 1995 and 1996 from Lagueux (1998). (Figure 5)

Data from Cuba on catch-per-unit effort per 100 net days are calculated from landing records for the hawksbill fishery at the Isle of Pines (Cuban Turtle Group, in litt. to A. Abreu, 15 February 2002) (Figure 6). After 1990, Cuba voluntarily phased down their annual harvest to 500 and this is reflected in the lower graphs of Figures 5 and 6.

Figure 5. Historical trends in abundance of hawksbill turtles in the Wider Caribbean. Note that the graphs have different scales on the Y axis.

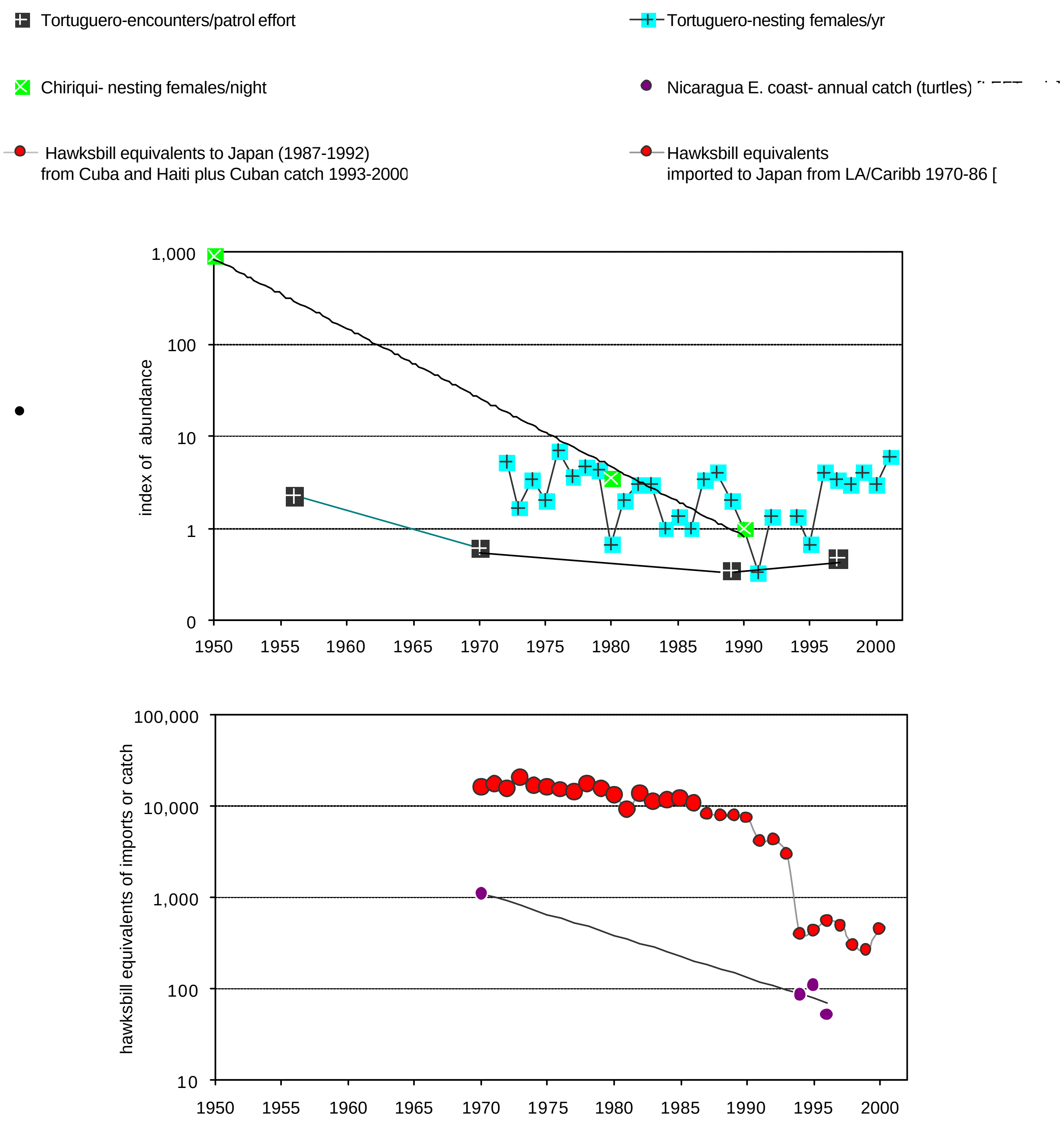
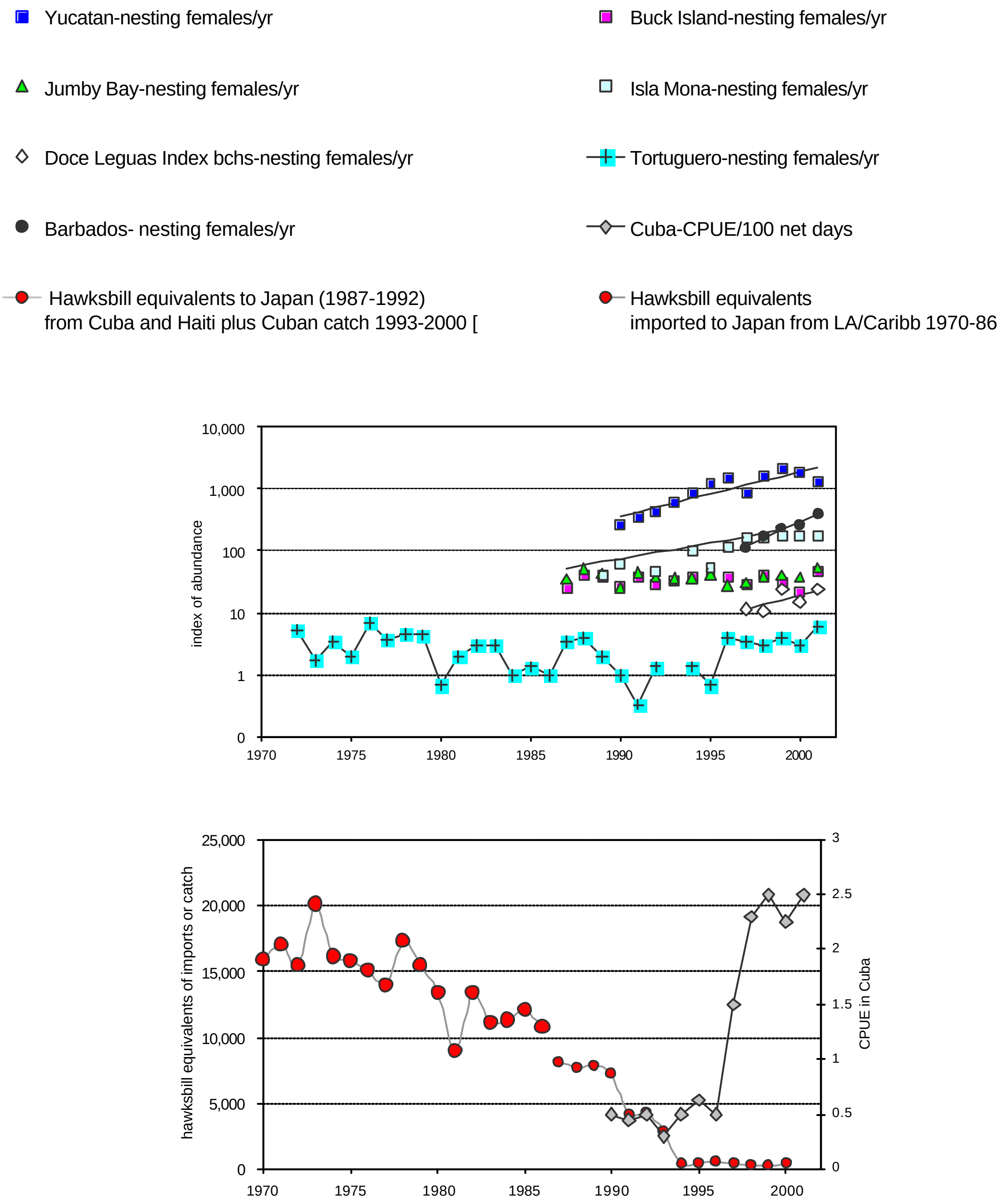


Figure 6. Recent trends in abundance of hawksbill turtles in the Wider Caribbean. Note that the graphs have different scales on the Y axis.



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Annex I - Sites of tagging and recapture, as well as countries visited during a migration track: hawksbill turtles flipper tagged or tracked with satellite telemetry in the Greater Caribbean (sensu SPAW Protocol); the majority of turtles were nesting females; only long-distance results from flipper tags are included[1]

		Country "visited" or last recorded during track[2]																																						
Country where tagged	Number of tagged turtles	Anguilla (UK)	Antigua & Barbuda	Aruba (Neth)	Bahamas	Barbados	Belize	British Virgin Is. (UK)	Cayman Is. (UK)	Colombia	Costa Rica	Cuba	Dominica	Dominican Republic	French Guiana	Grenada	Guadeloupe (Fr)	Guatemala	Guyana	Haiti	Honduras	Jamaica	Martinique (Fr)	México	Montserrat (UK)	Neth. Antilles (Neth)	Nicaragua	Panamá	Puerto Rico (US)	St. Christopher & Nevis	St. Lucia	St. Vincent & Grenadines	Suriname	Trinidad & Tobago	Turks & Caicos (UK)	USA Atlantic Caribbean	US Virgin Islands (US)	Venezuela	High seas	Total number of records[3]	Total number of "foreign visits"[4]	Total number of "foreign" countries visited[4]
Antigua & Barbuda	6		2										1													1				3										7	5	3
Bahamas	2											1																							1					2	2	2
Barbados	5												1			3	1															2		1				2	3	13	13	7
Belize	1						1																																	1	0	0
Costa Rica	13																				2						10	1												13	13	3
Cuba	14	1					1		1	1		9					1				3	1		1	1		1												2	23	14	11
Jamaica	4						1														2	3																	3	9	6	3
Mexico	11											1		1										6			1												2	11	5	4
Nicaragua	6																				1	1					4	1												7	3	3
Puerto Rico	4													3			1				1						1												2	8	8	5
US Virgin Is.	9							2				1		1												1	1		2		1									9	9	7
Total tagged	75	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Total records		1	2				3	2	1	1		12	2	5		3	3				9	5		7	1	2	18	2	2	3	1	2		1	1			2	12		- -	- -
Total "foreign visitors"[5]		1	0				2	2	1	1		3	2	5		3	3				9	2		1	1	2	14	2	2	3	1	2		1	1			2	12		- -	- -
Total countries		1	1				3	1	1	1		4	2	3		1	3				5	3		2	1	2	6	2	1	1	1	1		1	1			1	5		- -	- -
Total "foreign visitors' countries"[5]		1	0				2	1	1	1		3	2	3		1	3				5	2		1	1	2	5	2	1	1	1	1		1	1			1	5		- -	- -
Total values[6]		- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	103	78	48
Coral reef area (km²)[7]		30	240	50	3,150	100	1,330	330	230	900	970	3,020	100	610	*	150	250	*	*	450	810	1,240	240	1,350	*	420	710	570	480	180	160	140	*	100	730	1,250	200	480	- -	- -	- -	- -

[1] Data from sources listed in Meylan (1999a:Table 1) and Tables 1 and 2 herein

[2] The country where tagging occurred is not counted if the track indicated an immediate and directed departure

[3] One track can be recorded in multiple countries; "high seas" is included as a country

[4] "Foreign visits" and "foreign countries" include high seas but exclude the country where the transmitter was attached

[5] "Foreign visitors" and " foreign visitors' countries" include the high seas but exclude the country where the transmitter was attached

[6] Overall values for total sample for total "visits" and average visits/turtle

[7] Data on area of coral reef from Spalding *et al*.. (2001)

*Data on area from coral reef are not available in Spalding *et al*.. (2001), but value is insignificant

Annex II. Summary of information on growth rates of hawksbill turtles (*Eretmochelys imbricata*) in the wild. All measurements are straight carapace, from anterior notch to posterior tip ("SCLnotch-tip"). All studies used mark-recapture time intervals of more than 1 year, except for those from Barbados, Cuba, and Dominican Republic, which measured growth rate for intervals of about 6 months or more, and extrapolated to yearly growth rates those values of < 12 months (see source for further details)

	Average growth rate (cm/yr) ± SD (N) for each size class							**Range of capture-recapture intervals**	**Notes**	**Source**
Study area	**20<29**	**30<39**	**40<49**	**50<59**	**60<69**	**70<79**	**80<89**			
Bahamas		15.7**	5.9 (1)							- Bjorndal & Bolten, 1988
West Coast bank reef, Barbados	4.13 ± 1.24 (12)	3.48 ± 1.25 (20)	1.89 ± 1.45 (42)	1.44 ± 0.82 (16)	1.53 ± 0.75 (6)	0.17 ± 0.55 (4)		≥ 6 months	used average of initial and recapture size for grouping size class results	B. Krueger, unpubl
Doce Leguas + Isla de Pinos, Cuba	8.18 ± 0.79 (8)	8.14 ± 2.4 (23)	6.89 ± 2.19 (6)		1.35 ± 0.54 (2)	1.24 ± 1.5 (2)	0.83 ± 0.98 (8) (nesting)	≥ 6 months	used average of initial and recapture size for grouping size class results	Moncada & Nodarse unpubl.
Mona Is. Reef, Puerto Rico	2.63 ± 1.41 (46)	3.07 ± 1.77 (41)	2.9 ± 1.59 (22)	2.22 ± 1.08 (10)	0.74 ± 0.15 (3)	0.25 ± 0.13 (8)	-0.29 ± 0.02 (1)	> 12 months	compiled and averaged by 1 cm SCL intervals	Diez & van Dam, 2002
Mona Is. Cliff, Puerto Rico	2.65 ± 1.56 (33)	3.17 ± 1.77 (31)	2.64 ± 1.43 (11)	2.05 ± 0.63 (3)	1.39 (1)					
Monito Is. , cliff wall, Puerto Rico	6.48 ± 3.05 (21)	6.47 ± 3.44 (24)	5.35 ± 2.82 (11)	4.19 ± 2.1 (10)	3.91 ± 1.53 (6)	2.69 ± 0.43 (2)	1.33 ± 0.36 (3)			
Lanza Zó, Dominican Republic		8.84 ± 1.25 (5)						> 6 months		León & Diez, 1999
Cabo Rojo, Muelle Oeste, Playa Oeste, Dominican Republic	5.3 ± 1.45 (11)	4.04 ± 1.62 (5)						> 6 months		

* Confidence intervals calculated for an ? ∂f 0.05 by ± 1.96 x [? /? (n)]

** not plotted in Figure 5 because the value, based on a sample of one, is an anomalous outlier

*** Original data reported as curved carapace length (CCL), converted to straight carapace length (SCL) in Figure 6.

Annex III Status of hawksbill turtles (*Eretmochelys imbricata*) in 35 geopolitical units of the Caribbean region (adapted from Meylan, 1999a).

Geopolitical Unit	Population Estimates		Status/ Trends (Source)
	Number of Nests or Nesting Females Per Year	Comments (Source)	
Anguilla	No estimate available.	Nesting density low, based on interviews (Meylan, 1983).	Population depleted (Meylan, 1983).
Antigua/Barbuda	400-500 nests	Most significant nesting site is Jumby Bay, Antigua (see Annex II) (Fuller *et al*.., 1992).	Hawksbill populations in Antigua and Barbuda are considered “remnants” (Fuller *et al*.., 1992); number of nesting females at Jumby Bay appears stationary (J. Richardson, pers. comm.).
Aruba	No current nesting known.	Appropriate nesting habitat available but no confirmed nesting (Barmes *et al*.., 1993).	
Bahamas	No estimate available.	Surveys limited but no concentrated nesting known (Bjorndal, pers. comm.).	Stable (Higgs, 1984); considerable decline in last 50 years (Carr *et al*.., 1982).
Barbados	50-60 females	Estimate based on public reports, beach surveys, tagging program (Horrocks, 1992; J. Horrocks, pers. comm.).	Populations considered depleted (Hunt 1984) but numbers of nests are now increasing (Horrocks & Kreuger, unpub. data).
Belize	40-50 females	Most significant nesting site is Manatee Bar with 25 females per year (Smith *et al*.., 1992); 30-40 nests/yr at Sapodilla Cays (K. Holterman, pers. comm.).	Noticeable decline in the Belize hawksbill population (C. Miller, cited in Moll 1985).
Bermuda	No nesting known.	Burnett-Herkes, 1987	
British Virgin Islands	No estimate available.	3 nests in 1990 (6 islands surveyed); 10 nests in 1991 (10 islands surveyed); 61 nests in 1992 (12 islands surveyed). Surveys intermittent (Eckert *et al*.., 1992).	Stable (Clarke, cited in Groombridge and Luxmoore, 1989); “decline in stocks over recent decades” (Eckert *et al*.., 1992).
Cayman Islands	1 – 2 females/yr	Aiken *et al*.., in press	Breeding populations previously believed to be extinct (Groombridge & Luxmoore, 1989).

Geopolitical Unit	**Population Estimates**		**Status/ Trends (Source)**
	Number of Nests or Nesting Females Per Year	**Comments (Source)**	
Colombia	No estimate available.	Nesting sparse on mainland (Groombridge & Luxmoore, 1989). Total of 21 nests recorded in San Andrés Archipélago in 1996 (Cordoba *et al*.., 1998).	Nesting markedly decreased at Buritaca (mainland), now rare (Kaufmann, 1975). Marked decline on offshore cays (Carr *et al*.., 1982).
Costa Rica	< 25 nests/yr at Tortuguero. 1955 –2000	Nighttime surveys on 8 of 35 km of Tortuguero Beach (see Annex II) (Caribbean Conservation Corporation, unpub. data).	Continuous decline at Tortuguero from 1956 to 1991 (Bjorndal *et al*.., 1993).
Cuba	1700-3400 nests	Full extent of nesting unknown; maximum number of nests recorded on all beaches in any one year was 409 on 47 beaches (Moncada *et al*.., 1999).	Trends of nesting population unknown, but suspected to be declining in some areas (Carrillo *et al*.., 1999; Moncada *et al*.., 1999).
Dominica	No estimate available.	Six confirmed nests in 1984 (Edwards, 1984); nesting density low (Gregoire, cited in Groombridge & Luxmoore, 1989).	Nesting population decreasing (Gregoire, cited in Groombridge & Luxmoore, 1989).
Dominican Republic	310 females	Estimate based on aerial surveys and interviews conducted in 1980-81 (Ottenwalder, 1981, 1987).	Population decreasing (Ottenwalder, 1981, 1987).
Grenada (and Grenadines)	No estimate available.	Previous estimate of >500 females (Finley, 1984) not based on surveys, considered too high (C. Isaac, pers. comm. to M. Donnelly).	Trends unknown.
Guadeloupe (and St. Barthelemy, St. Martin)	No estimate available.	Nesting levels low, based on interviews (Meylan, 1983).	Definite decline in marine turtle population levels; 14 of 15 persons interviewed on Guadeloupe who had knowledge of turtles reported decline (Meylan, 1983).
Guatemala	380-760 nests	Estimate based on 53 observed nests (Rosales-Loessner, 1984). Needs verification.	Trends unknown.
Haiti	No estimate available.	Aerial surveys in 1982 and 1983 revealed total of 3 nests (Ottenwalder, 1996).	"..second most abundant species in late 1700s. Today, populations seem severely reduced and, although nesting numbers are unknown, these are probably low" (Ottenwalder, 1996).

Geopolitical Unit	Population Estimates		Status/ Trends (Source)
	Number of Nests or Nesting Females Per Year	Comments (Source)	
Honduras	No estimate available.	Aerial and ground surveys on mainland and offshore islands between 1982 and 1987 revealed only sparse nesting (Cruz & Espinal, 1987).	Numbers greatly diminished on mainland, badly depleted in Bay Islands (Carr *et al*.., 1982); hawksbill population has declined around Utila in last 10-15 yrs and throughout Honduras in last 10-20 years (Cruz & Espinal, 1987).
Jamaica	200-275 females	Beach surveys conducted 1991-1996 (R. Kerr, pers. comm.)	Nesting population decreasing (Haynes, cited in Groombridge & Luxmoore, 1989).
Martinique	245-375 nests	Estimate based on limited beach surveys, interviews (Dropsy,1987).	Marine turtle populations of Martinique “gravely threatened” (Lescure, 1987).
Mexico	2929 – 7843 nests/yr 1996 – 2000	Data from beach surveys conducted in Campeche, Yucatán, and Quintana Roo (Garduño *et al*.., 1999; V. Guzmán, M. Garduño, K.López, M. Medina, pers. comm.)	Population increasing over period 1977-1996 (Garduño *et al*.., 1999).
Montserrat	No estimate available.	Nesting incidental, based on reconnaissance of beaches and interviews (Meylan, 1983).	Trends unknown.
Netherlands Antilles (Bonaire, Curaçao, Saba, St. Eustatius, St. Maarten)	No estimate available.	Nesting rare (Meylan, 1983; Van Buurt, 1984; Sybesma, 1992).	“Hawksbills appear to be much depleted from their former numbers” (Sybesma, 1992).
Nicaragua	25 females	Basis of estimate unknown (Incer, 1984). Nietschmann (cited in Groombridge & Luxmoore, 1989) described numerous nesting sites on offshore cays.	Population under extreme pressure from exploitation (Nietschmann, 1981); 92% decline in harvest rate in 28 yrs (Lagueux, 1998).
Panama	No estimate available.	Nesting occurs at low density throughout Bocas del Toro Province and the Comarca de San Blas (Carr *et al*.., 1982; Meylan & Meylan, unpub. data; A. Ruiz, pers. comm.).	Chiriquí Beach, once considered best nesting beach in Caribbean (Carr, 1956), now hosts only occasional nesting (Carr *et al*.., 1982; Meylan & Meylan, unpub. data).

Geopolitical Unit	**Population Estimates**		**Status/ Trends (Source)**
	Number of Nests or Nesting Females Per Year	**Comments (Source)**	
Puerto Rico (Mona, Culebra, Vieques, mainland)	650 nests	Calculated from Eckert, 1995, Diez *et al*.., 1998, and K. Hall, in litt. See Annex II for Mona Island.	"depleted U.S. populations are not currently declining, but neither are there indications of recovery" (Eckert, 1995). Nesting population at Mona Island increasing (Diez *et al*.., 1998, C. Diez, pers. comm.).
St. Kitts/Nevis	No estimate available.	Low density nesting occurs on both islands (Meylan, 1983; Wilkins & Meylan, 1984; Eckert & Honebrink, 1992).	"..serious decline in numbers (of hawksbills) over the course of recent decades" (Eckert & Honebrink, 1992).
St. Lucia	11 females	Basis of estimate unknown (Murray, 1984). Nesting occurs widely but at low density (Carr *et al*.., 1982); nesting hawksbills of "medium abundance" (Butler, cited in Groombridge & Luxmoore, 1989); nesting in very low density (d'Auvergne & Eckert, 1993).	Hawksbill nesting population decreasing (Butler, cited in Groombridge & Luxmoore, 1989); "populations of all species are declining" (d'Auvergne & Eckert, 1993).
St. Vincent (and Grenadines)	< 20 females	Bullis, 1984 (estimate based on limited data from Morris, 1984). Hawksbills nest widely but everywhere in reduced numbers (Carr *et al*.., 1982).	"The consequence of hundreds of years of exploitation is a widely acknowledged decline in the abundance of sea turtles" (Scott & Horrocks, 1993).
Trinidad/Tobago	No estimate available.	Nesting levels described variously as rare, minimal, and regular (see Groombridge & Luxmoore, 1989).	Trends unknown.
Turks and Caicos Islands	200-275 females	Estimated from 37 observed nests (Groombridge & Luxmoore, 1989). Needs verification.	Nesting population decreasing (Garland, cited in Groombridge & Luxmoore, 1989).
United States (mainland)	1 -4 nests	Surveys cover > 1000 km of beach in Florida; there may be additional, low-level nesting in Florida Keys (Meylan *et al*., 1995; Statewide Nesting Beach Survey database).	Trends unknown.

Geopolitical Unit	Population Estimates		Status/ Trends (Source)
	Number of Nests or Nesting Females Per Year	Comments (Source)	
US Virgin Islands (St. John, St. Croix, St. Thomas, Buck Island Reef Nat'l. Monument)	~400 nests	Estimate calculated from Eckert (1995). For Buck Island Reef National Monument, St. Croix, see Annex II.	Local stocks depleted by intense commercial harvest of shell for export (1920-40s); "depleted U.S. populations are not currently declining, but neither are there indications of recovery" (Eckert, 1995). Buck Island stationary (J. Richardson, pers. comm.)
Venezuela	50 – 500 females	Rodriguez & Rojas-Suarez, 1995. Nesting occurs widely on offshore islands and is reported for three states on the mainland (Groombridge & Luxmoore, 1989).	Trends unknown.