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Hawksbill Turtles (*Eretmochelys imbricata*) in Cuba: An Assessment of the Historical Harvest and its Impacts

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Abstract. – Since the 1500s hawksbill turtles (*Eretmochelys imbricata*) have been harvested for food and tortoiseshell trade in Cuban waters. Between 1935 and 1994 an estimated 168,781 animals (8600 metric tons live body weight) were harvested. Starting in 1968 the harvest was managed as a commercial fishery in four fishing Zones (A–D) with the goal of sustaining an annual harvest indefinitely, rather than maximizing the catch in any one year. Catch effort was controlled and reasonably constant. The boundaries of the populations harvested were imprecisely known and probably varied between Zones. Between 1968 and 1990 an average of at least 4744 animals were harvested annually. Starting in 1990, as part of a fisheries rationalization program, the historical turtle fishery was phased down to the current (1995–98) traditional harvest of < 500 hawksbills per year from two harvest sites (one each in Zones B and D). Mean weight of hawksbills harvested decreased significantly from 51.1 kg in 1983–86 to 43.6 kg in 1987–95, although capture biases may be involved. Mean size varied at different times of year in Zone-specific ways. In Zone D, the mean size at all times of year appeared stable through the 1980s and 1990s. In other Zones, the mean size of turtles caught in some months was stable over the 1980s and 1990s and declined in other months. Sex ratios of animals caught were heavily female biased (> 80%) in all Zones, even those without significant nesting, and showed no significant change over time. The percentage of adults in the harvest continued to decline in Zone A but stabilized in Zone D. DNA analyses to date indicate that 67% and 64% of *E. imbricata* currently caught in Cuban waters (Zones B and D, respectively) could originate from nests in one part of Cuba (Zone A), regardless of whether intermediate growth stages were completed elsewhere. Others appear to originate from a variety of nesting and foraging areas within and outside of Cuban waters. The impacts and degree of sustainability achieved by Cuba's historical harvest of *E. imbricata* are largely unknown. The wild population was probably significantly reduced prior to the fishery being reorganized in 1968, but from the 1980s onward, when more extensive records were kept, the reduced wild populations continued to support a significant annual harvest without any further dramatic decline in abundance or change in sex ratio. A suite of more subtle and gradual declines were occurring, perhaps very significant to assessments of potential sustainability. Impacts of the Cuban harvest on regional Caribbean populations in the 1980s and 1990s are unclear, but the extent of nesting on various beaches monitored in the wider Caribbean suggest that although numbers of nesting females were probably reduced relative to past levels, sometimes greatly, regional trends were stable and possibly increasing rather than decreasing during the 1980s and 1990s.

Key Words. – Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; harvest; management; population dynamics; conservation; Cuba

Hawksbill turtles (*Eretmochelys imbricata*) occupy tropical and subtropical waters around the world and occur throughout the Caribbean, mainly in coastal waters (Witzell, 1983; Márquez, 1990; Baillie and Groombridge, 1996). They have a long history of being used for food, medicines, oil, and shell (Groombridge and Luxmoore, 1989). The thick, keratinized "tortoiseshell" scutes of *E. imbricata*, with attractive patterns and plastic-like consistency, have long been valued as raw material for artisans. Trade in tortoiseshell has occurred for hundreds of years and has provided commercial incentives for extensive and often uncontrolled wild harvesting around the world (Milliken and Tokunaga, 1987; Meylan, 1997; Carrillo et al., 1998a; CCMA, 1998). By the 1970s and 1980s, concerns about the status of wild populations led to protective legislation in many countries (Groombridge and Luxmoore, 1989). When combined with trade controls under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), harvesting for international trade gradually declined. Legal international trade ceased in 1993 when Japan's reservation on *E. imbricata* under CITES was relinquished.

Throughout the period of widespread commercial harvesting of *E. imbricata*, relatively few controlled management programs appear to have been implemented (Meylan, 1997). High levels of ongoing harvest can reduce wild populations greatly (e.g., harvesting all nesting females on

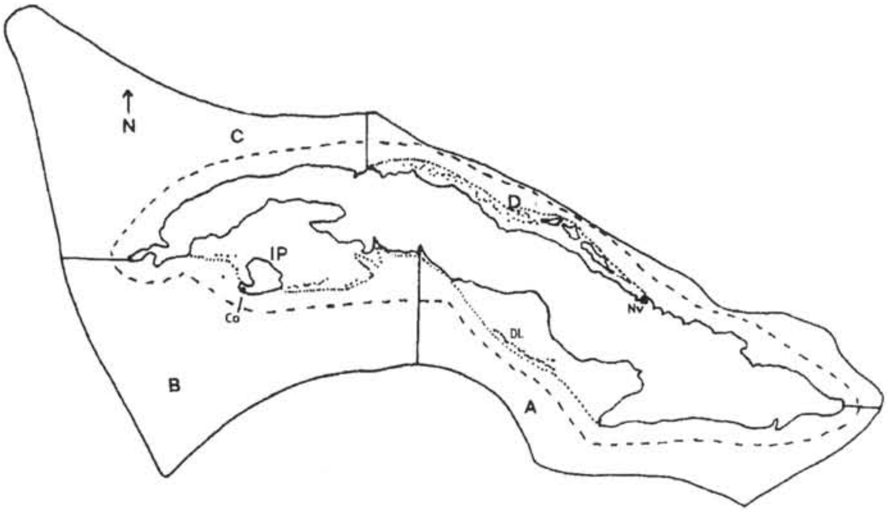

Figure 1. Cuba's territorial waters (broken line) and exclusive economic zone (solid line), subdivided into the 4 Fisheries Zones (A, B, C, D) used for managing the marine turtle fishery. IP = Isle of Pines; DL = Doce Leguas Keys, the main nesting area in Cuba; Co = Cocodrilos; Nv = Nuevitas. The dotted line is the 20 m depth contour.

particular beaches year after year [Meylan, 1997]), but relatively little is known about the impacts of other types and levels of wild harvest. Nor can the impacts be predicted with confidence from current population simulation models. Relatively few population parameters are known accurately and the dynamics of interactions between them, including density-dependent adjustments, are unknown (Chaloupka and Musick, 1996; Carrillo et al., 1998b).

From this perspective Cuba's historical hawksbill harvest is an important management case history. The rate of harvest was maintained below maximum levels and some records were kept on the size and sex-structure of harvested animals. Despite the quality of these data being uneven and the records incomplete, they provide unique insights into trends in the harvested population over time. These have application to assessments of sustainability and provide reference points for assessing the future status of *E. imbricata* in Cuban waters.

MANAGEMENT AREA

Cuba (Fig. 1) is the largest island complex in the Caribbean. It is about 1200 km long by 100 km wide and is associated with an archipelago of 2128 islands and atolls (total land area = 110,860 km^2). Some 16% of the 5120 km of mainland coastline and < 5% of the island coastline (3000+ km) are developed. The majority of Cuba's 12 million people (0.21% annual rate of increase in 1994) live on the mainland, where there is extensive agricultural development. Territorial waters comprise 111,400 km^2 and the exclusive economic zone an additional 259,200 km^2. Cuba thus has claim to 370,600 km^2 of Caribbean waters, referred to here generally as "Cuban waters." For the purposes of managing the marine turtle fishery these waters were subdivided into four fisheries Zones: A, B, C, and D (Fig. 1).

From the viewpoint of *E. imbricata* habitat, Cuba is a marine shelf with some 44,000 km^2 of shallow waters (< 20 m deep) containing coral reef ecosystems. These are more extensive on the sheltered southern coast (33,705 km^2 < 20 m deep) than along the northern coast (10,371 km^2 < 20 m deep), where the shelf drops off sharply to waters over 2 km deep. Surface sea temperatures are generally 1°C lower in the north (max. 28.8°C, min. 24.9°C) than in the south (max. 29.8°C, min. 25.9°C), which contains the main nesting and feeding areas for *E. imbricata* in Cuba.

Ocean currents surrounding Cuba are complex, with numerous countercurrents and seasonal influences (Carrillo and Contreras, 1998). In May–June strong currents (> 25 cm/sec) sweep from east to west across the southern coast, outside of the Doce Leguas Keys. They flow around the western extremity of Cuba before heading north. At this time on the north coast the dominant inshore flow is from west to east with moderate currents (< 25 cm/sec). By November, the direction of flow in both the south and north are almost completely reversed (Carrillo and Contreras, 1998).

HISTORY OF UTILIZATION AND MANAGEMENT

Early History. — When the Spanish first settled Cuba in the early 1500s, the indigenous people had well developed harvesting methods for marine turtles (*Chelonia mydas*, *Caretta caretta*, and *E. imbricata*), which included both nets and tethered *Remora* (suckerfish) (Direccion Politica De Las F.A.R., 1967; Baisre, 1987). Southern Cuba was recognized as containing commercially significant marine turtle resources (Fray Bartolome de las Casas, in *Historia de las Indias* [1525], quoted in Baisre, 1987; Pérez de Oliva, 1528; Depeñalver Angulo, 1635). Increased demand for *E. imbricata* shell in Europe in the 1700s and 1800s prompted increased harvesting and trade generally (Pearson, 1981; Fosdick and Fosdick, 1994), and the Doce Leguas Keys were identified as one of the earliest commercial harvest areas (Parsons, 1972). A market for live turtles existed in

Havana, to which some turtles were transported by coastal ship (Le Riverend, 1971). In the late 1800s at least some families were still emigrating to Cuba to establish turtle fishing enterprises (Carrillo et al., 1998d).

1936–1958. — In 1936, Decree Law No. 704 ("General Law of Fisheries") introduced closed seasons on turtle harvesting, which suggests concern about the sustainability of the harvests. In 1956, more explicit regulations about the utilization of all marine resources, including turtles, came into force (Decree No. 2724). The full extent of utilization during 1936–58 is unknown, but Cuban Customs Records indicate the export of some 14.7 metric tons of *E. imbricata* shell between 1935 and 1945, and 18.5 metric tons between 1950 and 1958 (no data are available for 1946–49). Carrillo et al. (1998a) assumed that it was likely that larger turtles were caught at this time (average around 55 kg) and used an estimate of 1.6 kg of shell (shell = 3.0% of body weight at 55 kg) to derive a minimum estimate of around 20,000 animals.

1959–1968. — Following the Cuban Revolution (1959), the Ministry of Fisheries (MIP) enacted new legislation to control utilization of marine resources. In 1960 (MIP Resolution 31-V) closed seasons for marine turtles were changed, and in 1961 (MIP Resolution 16-VI) the taking and consumption of sea turtle eggs and the disturbance of nesting females were prohibited. In 1968, MIP Resolution 117 established the marine turtle fishery as a formal managed fishery, in which harvesting and the accumulation and distribution of products and byproducts were controlled by the State. Between 1959 and 1968, 44 metric tons of *E. imbricata* shell were exported; these are the only data available on the extent of the harvest in this period. Carrillo et al. (1998a) assumed the same average size (1.6 kg per animal) which equates to a minimum estimate of some 27,500 individuals harvested. If the mean size of turtles caught was lower (45 kg; shell = 3.2% of live body weight; 1.44 kg/animal), the estimate would be higher (30,556 animals).

Table 1. Boats used in the Cuban turtle fishery from 1968 onward. At the start of the fishery mainly larger boats were used, but these were scaled down through the 1980s as efficiency increased.

Boat Type	Description
Ferrocento	Three-man; 12.9 m long; beam 4.05 m; 95 HP; inboard
Cayo Largo	Three-man; 18.3 m long; beam 4.56 m; 150 HP; inboard
Criollos	Three-man; old boats from before the Revolution; beam not taken into account; seven categories recognized based largely on length: A 5.79 m B 7.32 m C 7.32 < 8 m Cm 8–10 m D_1 10.06 < 18.28 m D_2 18.28 < 21.34 m D_3 21.34 < 21.43 m
Sigmas	Two-man; 10 m long; beam 3.2 m; 25 HP; inboard
Cherneras	Grouper fishing boat; Two-man; 5–7 m long; beam 1.78 m; 11 HP; inboard

Table 2. Types of nets used in the Cuban turtle fishery after 1968. Total fishing effort in terms of *Superficie* nets was based on studies indicating catch equivalents: 1 *Calamento* = 5.03 *Superficie* and 1 *Fondo* = 2.5 *Superficie*.

Net Type	Description
Superficie	Top net, 50–60 fathoms long, 12–15 meshes deep, 46–53 cm mesh size. Floats, with no lead line.
Calamento	Set net, 120–235 fathoms, 12–40 meshes deep, 38–48 cm mesh size. Set in areas from shallow to deep.
Fondo	Bottom net, 50–60 fathoms long, 12–15 meshes deep, 43–53 cm mesh size. Has heavy lead line to sink to the bottom, such that the floats are submerged and the net fishes the bottom layers.

1968–1990. — From 1968 onward the marine turtle fishery was subject to all management directives applied to other fisheries. The goal was to sustainably harvest turtle meat for domestic consumption and the prime unit of management was metric tons live weight of catch. The harvest was directed at adults rather than juveniles and at varying times minimum size limits in length (up to 60 cm SCL, 24 kg) were imposed with margins of error to allow for incidental take. How the harvest levels in 1968 were first established is unknown, but each year thereafter catch targets were varied up or down by the Committee of Fisheries Management or their equivalent. In formulating annual targets the Committee took account of the extent of the previous year's catch, changes in harvest techniques (net types and mesh sizes), new size limits, and any new research results. The goal was to sustain a harvest indefinitely and not simply to maximize the catch in any one year.

Catch targets were subdivided among the State's Fisheries Enterprises, which in turn coordinated the activities of a range of Fisheries Establishments (Cooperatives). All boats (Table 1) and nets (Table 2) were standardized and owned by the State. Various combinations of nets and boats were allocated to particular Cooperatives in order to meet their catch targets, and their performance was monitored (Table 3). Fishermen were subject to the same inspection procedures, enforcement procedures, and penalties applied to all Cuban fisheries.

Some Cooperatives operated from shore-based facilities and fished in near-coastal waters, whereas others operated from larger vessels in more open waters. Where refrigeration was not available turtle meat was salted and correc-

Table 3. Numbers of boats operating in the Cuban turtle fishery (1979–90) and live weight in metric tons (t) of *E. imbricata* catch per boat per year. Catch increased at an average rate of 0.18 metric tons per boat per year (linear regression, $r^2 = 0.67$; $p = 0.001$) (after Carrillo et al., 1998b).

	Zones				Total	Total	Catch (t)
Year	A	B	C	D	Boats	Catch (t)	per Boat
1979	21	15	24	32	92	202.9	2.21
1980	21	13	24	32	90	263.1	2.92
1981	18	14	24	29	85	253.1	2.98
1982	18	13	18	24	73	285.2	3.91
1983	16	12	18	25	71	263.3	3.61
1984	20	10	18	26	74	253.0	3.42
1985	16	10	16	25	67	321.6	4.80
1986	16	10	16	24	66	241.5	3.66
1987	13	10	16	24	61	277.4	4.55
1988	11	10	15	23	59	247.3	4.19
1989	12	8	15	22	59	244.9	4.15
1990	12	6	16	16	50	229.0	4.58

tions were derived and used for estimating live weight from salted and/or processed meat. The shell scutes of *E. imbricata* were removed from the carapace and plastron by water maceration and forwarded to Havana-based fisheries enterprises responsible for marketing. Carapace scutes were individually graded according to size, color, and imperfections (mainly the extent of barnacle growth) prior to marketing. Prime shell was subsequently exported and the remainder used domestically by local artisans.

Incidental catch of *E. imbricata* in other fishing operations occurred throughout the period of harvesting. The body weight of turtles caught as incidental catch did not usually enter the official fishery statistics for total live weight of turtles harvested. As a disincentive, fishermen outside of the turtle fishing industry did not receive payment for meat taken as incidental catch (the meat was consumed locally by the fishermen). However, the shell derived from incidental catch apparently did sometimes enter the stream of product from the dedicated turtle fishery, and as such would appear in some shell export records.

In the early 1980s a sampling program was introduced to collect more information on the population being harvested. At some landing sites resident biologists were responsible for data collection and at others the data were collected by MIP officers responsible for monitoring fisheries operations generally. The prime measurement at all sites was live body mass and at least some variation in the exact measure of length used at different sites occurred from time to time. The procedures for selecting samples were not rigidly defined and sometimes appear to have been the opportunistic measuring of animals landed when a technician was present.

During the period 1983–95, some 8711 *E. imbricata* were measured: Zone A, 4412; Zone B, 1345; Zone C, 1355; Zone D, 1499 (Carrillo et al., 1998a). Research expanded in the 1980s with increased attention to catch effort (Table 4), nesting (Moncada et al., 1998a) and general biology (Anderes, 1994; Espinosa et al., 1994, 1996; Moncada et al., 1998b). In 1985–86 the sampling program was expanded into what had been previously designated closed seasons in order to better document the reproductive cycles.

During the 23-year period from 1968 to 1990, the available data are insufficient to estimate precisely how many individuals were harvested and they are sometimes internally inconsistent. The people involved with the fishery itself operated independently of those handling the products and those responsible for exports. Furthermore, numerous changes in management practice occurred at all levels over time. The overall estimate of annual numbers harvested is presented in Fig. 2 and represents an average of at least 4744 animals per year for 1968 to 1990.

Records of the total live weight harvested each year indicate that between 1968 and 1982 (before the sampling program started), 3573.4 metric tons live weight were caught; no additional data on the mean size of turtles caught are available. Carrillo et al. (1998a) used a mean estimate of 55 kg per turtle (3.9 kg heavier than the mean size recorded from the sampling program in 1983–86), to obtain a minimum estimate of the numbers of turtles taken (64,972 individuals). This would equate to an estimated production of 104 metric tons of shell (all scutes included). The proportion of shell used domestically in this period is unknown, and the only Cuban export records available (for 11 of the 15 years) are rounded to the nearest metric ton. However, most shell exported (90.3%) went to Japan, and the Japanese import records are more precise. They indicate 89 metric tons were received over the 15 years (Carrillo et al., 1998a). This suggests a total of 99 metric tons were exported in total, which is broadly consistent with the estimated production of 104 metric tons. Some incidental catch is no doubt included in the export records, and changes occurred over time in the relative proportions of different scutes (carapace, plastron, marginals, etc.) exported.

Between 1983 and 1990, total live weight harvested (2078 metric tons over the 8 years) from each Zone was recorded annually, and the sampling program provided information on the mean size of turtles caught in each Zone. Carrillo et al. (1998a) used the percentage of the total live weight of catch from each Zone, and the mean sizes recorded from each Zone, to derive an estimate of the mean size of turtles harvested in Cuba for each year. This mean was stable between 1983 and 1986 (51.1 ± 0.76 [SE] kg; range, 49.6–52.5), which included the period when closed seasons were abandoned, and stable after 1987 (1987–95; 43.6 ± 0.58 kg; range, 40.2–45.4) (linear regression $r^2 = 0.002$; $p = 0.90$) when closed seasons were reintroduced, but a significant reduction in mean size recorded occurred between the two periods (t-test on means; $t = 7.41$; $p < 0.001$).

Table 4. Catch per unit effort assessment. "Nets" refers to "*Superficie* net equivalents" (see Table 2); WT = metric tons liveweight of *E. imbricata* caught; CN = Catch per net. Regression statistics (slope, r^2, p) indicate the only significant trend was an increase in catch per unit net in Zone D (after Carrillo et al., 1998b).

	Zone A			Zone B			Zone C			Zone D			Total		
Year	Nets	WT	CN	Nets	WT	CN	Nets	WT	CN	Nets	WT	CN	Nets	WT	CN
1988	513	96.5	.19	440	51.2	.12	750	30.9	.04	296	69.3	.23	1999	247.9	.12
1989	580	92.5	.16	513	52.4	.10	750	25.8	.03	296	75.2	.25	2139	244.9	.11
1990	543	98.6	.18	350	24.2	.07	750	35.0	.05	286	71.2	.25	1929	229.0	.12
1991	468	66.1	.14	350	24.7	.07	750	25.8	.03	211	58.5	.28	1779	175.1	.10
1992	388	84.6	.21	350	30.4	.09	750	21.1	.03	195	56.8	.29	1683	192.9	.11
Slope			+			–			–			+			–
r^2			0.05			0.49			0.35			0.90			0.31
p			0.71			0.19			0.30			0.01			0.33

Carrillo et al. (1998a) estimated the numbers of individuals harvested each year from the total live weight divided by the estimated mean live body mass (BM) (total 1983–90 = 44,142 individuals). Total shell production over this period was estimated (range: 3.2% shell mass at 40.2 kg BM to 3.1% shell mass at 52.5 kg BM) as 65.5 metric tons. Japanese import records indicate 48.5 metric tons were imported. The disparity could be accounted for by a wide range of potential biases: Cuban exports underestimated, mean size being larger than indicated by the sample data, total live weight caught being overestimated, increased domestic use, or changes in the proportion of shell exported each year. It is perhaps worth noting that if the mean size of turtles caught during this period was smaller than estimated by the sample data, the disparity between estimated shell production and Japanese imports would increase rather than decrease.

1990–1994. — In 1990, Cuba acceded to CITES and as provided for under Article XXIII, lodged a reservation for *E. imbricata*. This allowed Cuba to continue trading *E. imbricata* shell internationally with non-Party States and with those Parties that also held a reservation. CITES did not affect Cuba's domestic harvest; only its ability to trade *E. imbricata* shell internationally.

Independent of CITES, 1990 was also the year in which Cuba carried out an extensive rationalization of its fishing industries. This led to the allocation of fishing effort away from marine turtles (Fig. 2), a largely domestic harvest, towards more valuable export fisheries. This action was not motivated by decreasing stocks of turtles within Cuban waters *per se*, although is was clearly recognized that mean size of turtles caught was declining in some Zones and stable in others (see below). Cuba's main trading partner for tortoiseshell was Japan, which lifted its reservation on *E. imbricata* in 1992 (effective 1993). This closed Cuba's export market for shell, and fishing effort was further diverted away from marine turtles. In 1994, all Cuban waters were completely closed to marine turtle harvesting (MIP Resolution 298) with the exception of traditional harvest sites at Isle of Pines (1994, MIP Resolution 300) and Nuevitas (1995, MIP Resolution 3).

During the period 1991–94, 530 metric tons live weight were reported and the mean size ranged between 40.2 kg and 45.4 kg per year: Carrillo et al. (1998a) estimated a minimum of 12,167 *E. imbricata* were harvested. In 1991 and 1992, 10.4 metric tons of shell were exported to Japan (1991–92 harvest; 8261 individuals) and the remaining shell was stockpiled (1993–94 harvest; 3906 individuals).

The total recorded harvest between 1935 and 1994 was reported by Carrillo et al. (1998a) as 8600 metric tons live weight, which they estimated to have come from a minimum of 168,781 animals.

1995–1998 (Current Management). — Since 1994, marine turtle harvesting has been restricted to the Isle of Pines and Nuevitas (Fig. 1). On the Isle of Pines, the harvest occurs at Cocodrilos (formerly Jacksonville), a remote settlement on the southwest coast with two harvest sites (Punta Pedernales and El Diablo). At Nuevitas harvesting occurs at four sites (Punta Ganado, Cayo Romano, Cayo Guajaba, and Los Pinos). At all locations turtle fishing has been the main economic activity in living memory. Cocodrilos (1996 human population = 332) was founded by turtle fishermen who immigrated from the Cayman Islands in 1885. The central economic activity of the community has been turtle fishing for 113 years.

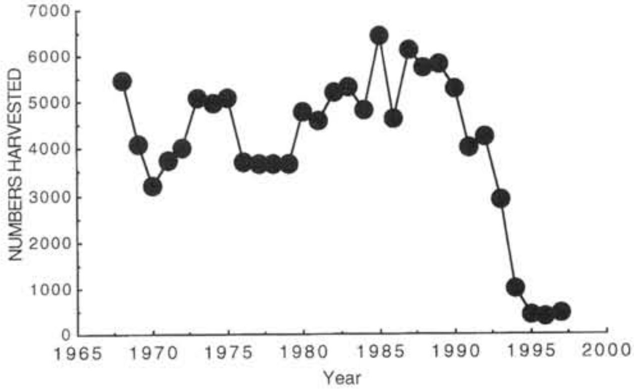

Figure 2. Estimated annual harvest of *E. imbricata* in Cuban waters, 1968–97 (see text). In 1990 the harvest was deliberately phased down, and since 1995 has been restricted to two traditional harvest sites.

The combined annual harvest from both sites is now less than 500 *E. imbricata* per year, around 10% of the annual Cuban harvest between 1968 and 1990 (Fig. 2). Additional legislation has strengthened prohibitions on taking marine turtles (1996, Decree Law 164), restricted fishing activities in and around the Doce Leguas Keys (1996, MIP Resolution 563), and established a series of Resolutions strengthening environmental management generally (Carrillo et al., 1998c). The level of management and monitoring associated with the traditional harvest has been increased greatly, and continues to improve as the national management program is refined.

At both traditional harvest sites there is a closed season for three months (May–July) and harvesting within the open season is often reduced by bad weather. Under the umbrella of the maximum harvest limit (500 per year) both areas operate under a catch plan. At Isle of Pines this consists of four cherneras boats (Table 1) with < 15 bottom and/or surface nets per boat (Table 2). Nets are set within 400 m of the shore and turtles are landed at the local processing facility. At Nuevitas the catch-plan consists of four cherneras boats (Table 1) with < 400 m of calamento nets per boat. These are set perpendicular to the shore, adjacent to where the fishermen reside. Turtles are measured and weighed before being transported to the processing facility at Nuevitas.

A unique field identification number (FIN) coded for capture site (Isle of Pines = IP; Nuevitas = PG, CR, CG, or LP), year, and consecutive number (e.g., IP/96/001), is written on the shell scutes of each turtle caught, and the following data are recorded: straight carapace length; straight carapace width; curved carapace length; curved carapace width; general condition; live body weight; presence of tags; sex; presence and size of enlarged follicles and/or oviductal eggs; number and weight of different shell scutes, and other products produced (meat, skin). Records are kept in triplicate data books, with one copy forwarded to MIP in Havana, one kept at the harvest sites, and one at the processing facility (Carrillo et al., 1998d).

After processing, the meat is deboned, reweighed, packed in plastic fish crates and chilled (< 10ºC); the skin is dried (after salting). The plastron and carapace are placed in individual mesh bags and submerged in water for 5–10 days. All shell scutes (plastral, dorsal, and marginal) are recovered, weighed, and repacked in plastic bags provisionally sealed with the FIN. Meat, skin, and bags of scutes are collected regularly by the Fishing Enterprises. Meat and skin are transferred to the Ministry of Interior Trade for distribution within Cuba and for tanning and manufacture into items for domestic consumption. The scutes are sent to the central store at Cojimar, Havana. Here, scutes from each individual *E. imbricata* are laid out on a light table, graded, and photographed with a digital camera. The scutes are recounted, weighed, and repacked in a heat-sealed plastic bag. A non-reusable CITES label (issued by the Cuban CITES Management Authority) containing all relevant data is included in each photograph, and later fixed to the bag. The digital images are transferred to computer and, if necessary, allow scutes from individual turtles to be identified by size, shape, and unique color pattern (Carrillo et al., 1998d). These images also provide a permanent record of growth rings on the dorsal scutes (Carrillo et al., 1998b), which give an indication of age (CCMA, 1998).

All scutes collected since 1993 have now been photographed, sealed in plastic bags, and stockpiled at Cojimar. Stocks as of June 1998 are approximately 7 metric tons, and comprise shell from the 1993–94 harvest (3906 individuals) and the traditional harvest from 1995–97 (approximately 1500 animals). The smaller mean size of shell (1.26 kg/animal) reflects smaller animals included in the harvest from Zone A (1993–94) prior to the cessation of harvesting, when minimum size limits were relaxed (Carrillo et al., 1998a).

POPULATION TRENDS

The impacts of almost 500 years of harvesting *E. imbricata* in Cuban waters are and will remain largely beyond quantification. Only in the period 1968–95 was the harvest managed as a controlled fishery, and most sample data are from 1983 to 1997 — a small window in time for evaluating a population subjected to continuous harvest at varying levels for hundreds of years.

To examine trends in the harvest over time the limitations of the sample data collected since 1983 are important. First, the information collected was very basic and was sometimes restricted to live body mass, sex, and month of capture. Second, different people in different parts of Cuba were involved in collecting data and measuring lengths, and they did not necessarily follow the same exact procedures. Third, the possibility of measurement bias can rarely be excluded. Fourth, the data refer to a wild commercial harvest over time, which was subject to a suite of unrecorded biases and changes due to weather, management directives, varying closed seasons, experience, etc. The results shed light on major trends over time at a coarse rather than fine level of resolution.

The sample data for 1984–86 are extensive and involve large sample sizes spanning most months, in all four Zones. The intensity of sampling between 1986 and 1997 varied greatly within and between Zones, which confounds analyses of the total Cuban harvest from year to year. More records are available from Zone A than from other Zones, but they only extend to 1993 (harvesting ceased in 1994). Few data are available for Zone C after 1987. The records for Zones B and D extend to 1997, but there are gaps for some years and some months and the areas of harvest were changed and reduced in 1994.

Live body mass is not as reliable a measure of size as carapace length, because it can vary significantly with reproductive condition. However, it was the primary measure upon which the harvest was based. Straight carapace length was measured for many animals, but endpoints are thought to have varied. The results presented here rely mainly on mass, but length measures are used to check generally whether or not some trends are consistent.

Reproductive data recorded from females were very basic. Their status was recorded as: "shelled eggs" (eggs in the oviducts, which almost invariably occurred in animals also containing a complement of large ovarian follicles); "unshelled eggs only" (ovarian follicles that were considered large or mature, although no discrete size was stipulated, but no oviductal eggs); or "no eggs" (no large or mature follicles or oviductal eggs). The data are suitable for examining broad trends, but not for detailed interpretation of reproduction.

Based on all sample data, the mean multiple regression relationship predicting live body mass (BM in kg) from recorded lengths (SCL?; L in cm), and accounting for whether the animals were recorded as reproductively active or not (RA; animals with enlarged follicles or oviductal eggs coded as 1, and others as 0) is: $BM = -12.92 + 0.308L + 0.00677L^2 + 6.44RA \pm 10.55$ kg ($r^2 = 0.66$; $p < 0.0001$; range of $L = 40$ to 101 cm; $n = 8198$). This relationship indicates that the mean reproductively active animal caught was 6.4 kg heavier than the mean non-reproductive animal. The mean formula for predicting L (in cm) from BM (in kg), without accounting for reproductive condition (RA), is: $\ln L = 3.1452 + 0.2955 \ln BM \pm 0.0950$ cm ($r^2 = 0.69$; $p < 0.001$; range of $BM = 6$ to 100 kg ; $n = 8198$).

Table 5. Variation in the mean body mass and straight carapace length (SCL) of *E. imbricata* harvested from the four Fisheries Zones within Cuba. Data are from 1985–86, in which *E. imbricata* from all Zones were sampled in all months.

	Body Mass (kg)			SCL (cm)		
	Mean	SE	*n*	Mean	SE	*n*
Zone A	37.37	0.47	1094	64.98	0.31	1094
Zone B	43.97	0.67	772	68.11	0.38	772
Zone C	55.45	0.63	999	74.18	0.41	1091
Zone D	49.80	0.65	594	78.73	0.33	594

Table 6. Distribution and size of monthly samples of *E. imbricata* from Zone A in which individual body mass was measured. * Indicate missing data or closed seasons.

Year	'83	'84	'85	'86	'87	'88	'89	'90	'91	'92	'93	Total
Jan	*	17	22	7	73	48	40	37	31	*	19	294
Feb	*	21	6	89	52	58	13	35	9	6	11	300
Mar	*	*	19	76	137	59	19	24	42	13	48	437
Apr	*	4	45	129	125	21	42	35	16	3	18	438
May	*	24	48	61	159	40	27	25	38	3	44	469
Jun	*	2	24	25	*	27	47	26	37	26	46	260
Jul	*	4	47	19	*	15	75	28	19	13	1	221
Aug	*	2	53	21	*	37	105	78	108	21	70	495
Sep	*	180	39	14	219	*	*	*	*	18	*	470
Oct	2	44	57	44	105	*	*	*	2	23	*	277
Nov	52	30	37	91	98	*	*	*	*	*	*	308
Dec	25	19	60	61	73	50	25	38	11	7	*	369
Total	79	347	457	637	1041	355	393	326	313	133	257	4338

Significant seasonal fluctuations in the mean size of *E. imbricata* caught in all Zones, in all years, was strikingly apparent. To make comparisons over time for any particular Zone, subsets of data need to be selected where sample data existed for the same month or group of months, in each Zone, over varying time periods. In some cases this has been done by combining data over a number of years and comparing the mean size of *E. imbricata* caught at the start and end of a harvest period, for the same months or groups of months. In other cases data for some individual months or groups of adjacent months span most years since 1983, so that the pattern of change over time, rather than just the differences between the start and finish of the harvest period, can be examined. The available data do not allow Zone-specific trends to be examined in the same way, over the same time periods, for all Zones.

Zone-Specific Trends

From 1983 onward, the mean size of *E. imbricata* caught in Cuban waters varied significantly and consistently between Zones (e.g., Table 5; compare Figs. 3a, 4, 5, 7a, and 8). This indicates Zone-specific harvests were either not randomly harvesting the same homogeneously distributed population, or if they were, they were targeting different segments of it. Animals caught in Zones A and B tended to be smaller than those caught in Zones C and D. Zones A and B contain 75% of the shallow waters within Cuba (Fig. 1) where more juvenile *E. imbricata* appear to reside and were caught in the harvest (Carrillo et al., 1998e). In Zones C and D, most harvesting occurred in what appears to be near-coastal "transit" sites in which generally larger animals were caught moving past particular sites. If the mean size of *E. imbricata* resident and feeding in a Zone is smaller than the mean size of *E. imbricata* moving through a Zone, the relative proportions of resident, feeding, and transit areas in a Zone, and seasonal changes in movement, could all have been influencing the mean size of turtles caught.

Zone A. — This Zone (Fig. 1) was the major historical harvest site in Cuba for *E. imbricata*. Between the early 1980s and protection in 1994, it sustained a harvest of around 2000 animals per year (Carrillo et al., 1998a). Zone A contributed 36.7% of the total live weight of *E. imbricata* harvested in Cuba between 1983 and 1990 (Carrillo et al., 1998a). Relative to the other Zones within Cuba, a much higher proportion of *E. imbricata* in Zone A may have emanated from nests in Zone A, and a higher proportion of animals caught in the harvest appeared to reside in Zone A for longer periods of time. Analysis of DNA samples from nesting and foraging populations (Bass, 1997; CCMA, 1998; Díaz-Fernández et al., 1999) indicated that 82% of foraging animals have the same haplotypes as the local nesting population (Díaz-Fernández et al., 1999). Of the 10 haplotypes so far identified in Zone A from nesting and foraging populations, 2 (one nesting and one foraging) have not yet been identified elsewhere in Cuba.

Tagging studies, although limited, indicated that a high proportion of *E. imbricata* caught, tagged, and released in Zone A were subsequently recaught in Zone A. None tagged in Zone A were recaptured in the other Zones (Moncada et al., 1998b). Recent satellite tracking of three nesting females in Zone A (Carrillo, 1998; unpublished data) has shown that two females remained in Zone A after nesting and one left Cuban waters and traveled to the Miskito Banks off Hondurus and Nicaragua.

Throughout the period of harvesting and today, juvenile *E. imbricata* have always been reported as common in the shallow reefs of Zone A (MIP, unpublished data). If the developmental stages of *E. imbricata* hatched in Zone A are spent in pelagic waters (Bjorndal, 1996) and/or in feeding areas outside Cuba, then significant numbers appear to return to Zone A to grow, and if they subsequently leave, return to nest.

More animals were measured in Zone A than in any other Zone, although the extent of sampling varied greatly between months and years (Table 6). Large sample sizes for all months in 1984–86 form a baseline for comparing mean sizes in 1990–93:

Seasonal trends in the mean body mass of turtles caught each month were apparent in both 1984–86 and 1990–93 (Fig. 3a). Turtles caught in the earlier months of the year were smaller than those caught in the later months, with varying patterns of change between them (Fig. 3a). For example, turtles caught in January–April in 1984–86 (mean

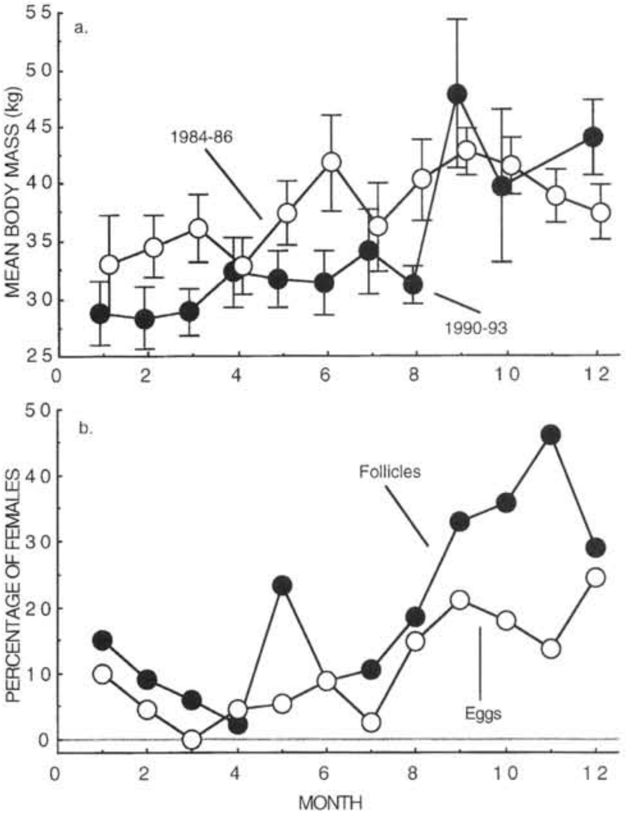

Figure 3. Monthly mean body mass (± 2 SE) of *E. imbricata* sampled in 1984–86 (○) and 1990-93 (●). Samples sizes are in Table 6 (top, a). Monthly percentage of female *E. imbricata* > 75 cm SCL sampled in Zone A (1985–86) that had enlarged follicles (●) and oviductal eggs (○) as reported by Moncada et al. (1998a) (bottom, b). The peak of nesting in Zone A occurs in September–December (Moncada et al., 1998a, 1999). 1 = January, 2 = February, etc.

of means = 34.13 ± 0.77 kg, $n = 4$) were significantly smaller than those caught in September–December (mean = 40.20 ± 1.21 kg; t-test, $t = 4.24$; $p < 0.01$) and the same trend was apparent in 1990–93 (Jan–Apr mean = 29.58 ± 0.92 kg, $n = 4$ vs. Sep–Dec mean = 43.88 ± 2.33 kg, $n = 3$; t-test, $t = 6.397$, $p < 0.0001$). Insufficient sample data were available for November which is not included in the September–December means.

These seasonal trends in body mass are correlated with the reproductive cycle (Fig. 3b). They appear to reflect changes in the mean lengths (SCL) of animals caught and are not simply increases in mass related to reproduction. For 1984–86 the mean monthly lengths recorded for January–April (64.09 ± 0.86 cm, $n = 4$) were smaller, but not significantly so, than those recorded for September–December (67.69 ± 1.29 cm, $n = 3$) (t-test, $t = 2.32$, $p < 0.1$). In 1990–93, the difference in recorded mean lengths between these two periods was highly significant (Jan–Apr mean = 60.88 ± 1.03 cm, $n = 4$; Sep–Dec mean = 71.04 ± 1.01 cm, $n = 3$; t-test, $t = 6.84$, $p < 0.0001$).

That heavier and longer animals tended to be caught during the breeding season, which peaks in September–December (Moncada et al., 1999) could indicate capture biases and/or the movement of larger animals into Zone A for nesting, from outside Cuba or from other Zones in Cuba.

For the eight months January to August (Fig. 3a), the mean mass of animals caught per month in 1984–86 was significantly greater than for 1990–93 (paired t-test; $t = 4.8071$, $df = 7$, $p = 0.002$), indicating a reduction in the mean size of *E. imbricata* caught during the non-reproductive season, probably due to harvesting. The same trend was apparent in recorded lengths (paired t-test: $t = 3.30$, $df = 7$, $p = 0.013$). Recorded monthly mean lengths (SCL, in cm) for 1984–86 and 1990–93, respectively, were as follows: January, 64.15, 59.61; February, 64.78, 60.49; March, 65.73, 59.50; April, 61.70, 63.90; May, 66.56, 61.98; June, 69.31, 61.67; July, 66.49, 65.77; August, 66.30, 63.09; September, 70.62, 71.44; October, 68.09, 69.12; December, 64.33, 72.55.

For September–December (Fig. 3a) the mean monthly mass of turtles caught in 1990–93 was not significantly different from 1984–86 suggesting relative stability in the mean size of turtles harvested during the reproductive season over this period (paired t-test; $t = 1.26$, $df = 2$, $p = 0.33$). The same trend was apparent in recorded mean monthly lengths (paired t-test, $t = 1.38$, $df = 2$, $p = 0.30$). The apparent increase in variablity in 1990–93 relative to 1984–86 was not significantly different for any month (F-tests, $0.05 > p < 0.10$).

Mean size of turtle harvested in April 1984–86 declined relative to the mean size in March during 1984–86 (Fig. 3a), whereas in 1990–93, the mean size in April increased relative to March in 1990–93. That is, the mean size in April was almost identical in 1984–86 and 1990–93. If the general decrease in mean size over time during the early parts of the year does reflect changes in the resident population, the apparent stability in April could indicate a pulse of animals moving into Zone A at this time of year.

In contrast to Fig. 3a, which examines differences in mean monthly size between two periods of time, Fig. 4 demonstrates changes in mean size as a function of year, for those months in which samples were available for all years. The mean size of turtles caught between January and August declined gradually and linearly between 1984 and 1993 (linear regression, $r^2 = 0.89$, $p < 0.0001$). In the September–

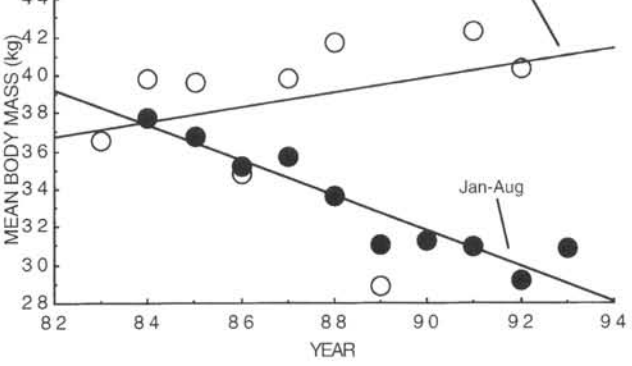

Figure 4. Mean body mass of *E. imbricata* caught in Zone A (mean of monthly means) as a function of year, for animals caught in January–August (●) and December (○). Lines are linear regressions indicating general trends which reach statistical significance for January–August but not December (see text).

Table 7. Numbers of *E. imbricata* harvested at the Isle of Pines, in Zone B (1983–97) for the months in which harvesting took place. Measurements of animals harvested in 1987 and 1988 are missing. * Indicates no harvest undertaken. r^2 and p refer to linear regressions against time indicating general trends.

	Month				
Year	Jan	Feb	Oct	Nov	Dec
1983	8	10	69	52	24
1984	24	22	72	25	23
1985	12	18	36	45	16
1986	15	11	55	52	48
1989	18	19	103	27	23
1990	15	16	83	40	25
1991	20	39	70	33	20
1992	5	21	73	58	38
1994	5	22	16	38	49
1995	17	28	58	48	22
1996	*	*	62	44	10
1997	5	10	57	20	*
r^2	0.16	0.08	0.04	0.01	0.00
p	0.20	0.36	0.50	0.73	0.96

December period, only data for December were complete (Table 6); no significant change in mean size between 1983 and 1992 was recorded, despite many more smaller turtles being included in the harvest in 1989 (minimum size limits were relaxed).

As reported by Carrillo et al. (1998e), there is no doubt that the number of adult females caught annually in Zone A declined during the period of harvest. For the months in which comparable data are available (February to March), which is outside the main reproductive season and may be sampling more of the resident population, 592 females > 60 cm SCL were sampled in 1984–87 and 316 between 1988–93. In 1984–87, 22.6% were greater than 75 cm SCL (50% maturity; Moncada et al., 1999) and this declined to 17.4% in 1988–93 (contingency table; $\chi^2 = 3.42$; $p = 0.064$). However, larger females (80–97 cm SCL) declined from 8.1% to 4.7% (contingency table; $\chi^2 = 3.60$; $p = 0.058$) over the same period.

Zone B. — This Zone (Fig. 1) contributed 18.1% of the total Cuban harvest of *E. imbricata* between 1983 and 1990. Zone B contains shallow waters and off-shore islands used for nesting (Moncada et al., 1998a), but the main sampling site was the transit site at Cocodrilos on the Isle of Pines (Fig. 1). At this site a higher percentage of *E. imbricata* originating from nests outside Cuba appear to be caught.

DNA analyses indicate 67% of animals recently sampled at Cocodrilos (77 of 115) contain haplotypes found in the nesting areas in Zone A (Díaz-Fernández et al., 1999). Nesting haplotypes from Zone B are yet to be determined. Of the 14 haplotypes so far identified, 12 are shared with other parts of Cuba and 2 have so far not been identified within Cuban waters. The range of haplotypes ($n = 14$) among harvested animals is greater than in Zone A foraging ($n = 9$) and nesting ($n = 5$) populations (Díaz-Fernández et al., 1999).

Two *E. imbricata* caught in Zone B had been tagged in Mexico (Moncada et al., 1998b) and 10% of animals currently caught in Zone B have haplotypes so far known only from Mexican nesting areas (Bass et al., 1996; Bowen et al., 1996; Moncada et al., 1998b; Díaz-Fernández et al., 1999).

Four of six animals fitted with satellite tracking transmitters at Cocodrilos (Isle of Pines; Fig. 1) have left Cuban waters (CCMA, 1998; Manolis et al., 1998). One traveled from the Isle of Pines to the southeastern extremity of Cuba via the Cayman Islands (ca. 880 km; CCMA, 1998). One swam northwest into the Gulf of Mexico and then southwest to the Yucatan Peninsulsa (ca. 1150 km), where it remained until transmissions ceased. One (the only male) swam southeast around the coast of Jamaica and then continued to a location between Montserrat and Guadeloupe (ca. 2450 km). The fourth headed southwest towards Belize, and then southeast to the coast of Colombia (ca. 2350 km) (Manolis et al., 1998). In all cases the individuals moved more rapidly and spent more time on the surface (giving better locations) when in deep waters.

The most complete set of monthly data for examining trends in Zone B are from January–February and October–December (Table 7; Fig. 5). Data for 1987 and 1988 were collected but the record books have been lost. The available data for Zone B are mostly live body mass; few measures of length were made.

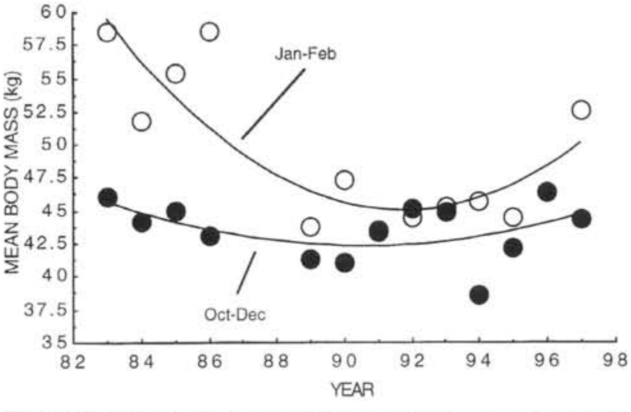

Figure 5. Mean body mass of *E. imbricata* (mean of monthly means) caught at Cocodrilos (in Zone B), 1983–97, for January–February (○) and October–December (●). Lines are polynomial regressions indicating general trends, which are statistically significant for January–February but not for October–December (see text).

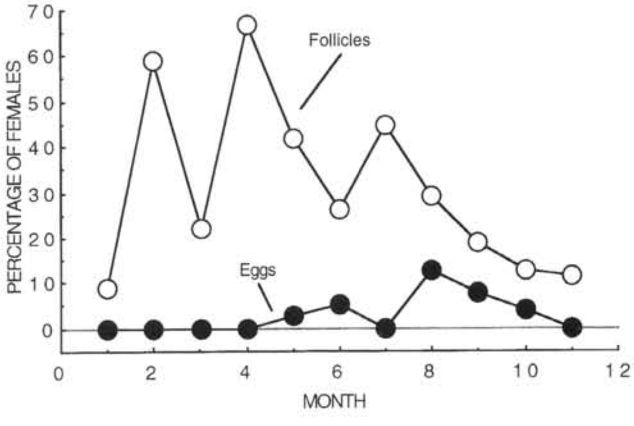

Figure 6. Percentage of female *E. imbricata* > 75 cm SCL sampled each month in Zone B (1985–86) that had enlarged follicles (○) and oviductal eggs (●) (after Moncada et al., 1998a). 1 = January, 2 = February, etc.

Seasonal variation between the early (January–February; larger animals) and late (October–December; smaller animals) parts of the year was apparent, but the extent of the difference decreased over time (Fig. 5). For the 4 years 1983–86 the mean seasonal difference (Jan–Feb vs. Oct–Dec) was 11.4 kg (means of annual means = 56.01 ± 1.58 kg for Jan–Feb and 44.58 ± 0.64 kg for Oct–Dec; paired t-test, t = 6.97, df = 3, $p = 0.006$). For the 9 years between 1989 and 1997 the mean seasonal difference was 2.8 kg (means of annual means = 45.82 ± 1.04 kg for Jan–Feb and 42.98 ± 0.82 kg for Oct–Dec; paired t-test, t = 2.65, df = 7, $p = 0.03$).

Between 1983 and 1997 (Fig. 5) the mean size of turtles caught early in the year (January–February) declined between 1983–89, stabilized between 1989 and 1995, and may now (1997) possibly be increasing (Fig. 5). However, this possible increase reflects limited data from only 15 animals in 1997 and no harvest in 1996 (Table 7); ongoing monitoring is needed to determine whether this apparent increase is real. The data are significantly better modeled by a polynomial regression ($r^2 = 0.72$, $p = 0.003$) than a linear regression, even if the 1997 data are excluded.

In contrast to the decline in mean size over the harvest period of animals caught early in the year (January–February), the mean size of those caught later in the year (October–December), in the non-reproductive period, appears to have remained relatively stable from 1983 to 1997 (linear regression; $r^2 = 0.03$, $p = 0.55$; Fig. 5).

The larger mean mass of turtles caught early in the year (January–February) in Zone B correlated with a peak of animals with enlarged follicles (Fig. 6), but not animals with oviductal eggs. The peak of nesting in Zone B appears to be June–August (Moncada et al., 1999).

As reported by Carrillo et al. (1998e), the number of adult females declined in Zone B, but sample data with greater than 10 per months are more limited (February–March, 1984–89). In 1984–86 and 1988–89, 55 and 17 females, respectively, of > 60 cm SCL were sampled. In 1984–86, 70.9% were greater than 75 cm SCL and in 1988–89 this had declined to 29% (contingency table; $\chi^2 = 9.41$; $p = 0.0022$). Larger females (80–93 cm SCL) declined from 51% to 12% (contingency table; $\chi^2 = 8.19$; $p = 0.0042$) over the same period.

Comparison of general trends between Zones A and B indicates the following.

1. In Zones A (Figs. 3a and 4) and B (Fig. 5) the mean size of *E. imbricata* caught early in the year declined over time.

2. In Zones A (Figs. 3a and 4) and B (Fig. 5) the mean size of *E. imbricata* caught late in the year remained relatively stable over time.

3. In Zone A the largest animals were caught late in the year (Fig. 3a) whereas in Zone B (Fig. 5) they were caught early in the year.

4. In Zones A and B the period in which larger animals were caught corresponded with the period in which high percentages of reproductively active females were caught (Figs. 3b and 6).

5. In Zone B, the time at which the largest and most reproductively active females were caught did not correspond with the Zone-specific time of nesting, whereas in Zone A it did.

6. The peak months of nesting in Zones A and B (November and July, respectively) are both associated with an increase in the percentage of turtles caught with enlarged follicles and a decrease in the percentage caught with oviductal eggs (Figs. 3b and 6).

7. In both Zones, the percentage of adult females caught during the harvest, in the early part of the year, declined over time.

Zone C. — This Zone contains transit sites, foraging areas, and nesting areas (MIP, unpublished data). It contributed 17.7% to the historical Cuban harvest between 1983 and 1990, but no tagging studies, satellite tracking, or DNA analyses have been carried out in this Zone, where turtle harvesting no longer occurs.

The sample data for Zone C are restricted to 1983–86 and cannot be used for examining changes in mean size over time. Seasonal trends in the mean size of turtles caught in 1983–86 were similar to Zone B. Mean size between February and August (mean of monthly means = 56.11 ± 1.07 kg and 74.3 ± 0.76 cm SCL), was significantly greater than for those caught between September and January (46.0 ± 2.06 kg and 65.3 ± 0.46 cm SCL) (mass: t-test, t = 4.75, $p < 0.001$; SCL: t = 9.03, $p < 0.001$). Between 1984 and 1986 the percentage of mature females increased (Carrillo et al., 1998e), but probably declined later. As in Zones A and B, larger and heavier animals were correlated with the times of

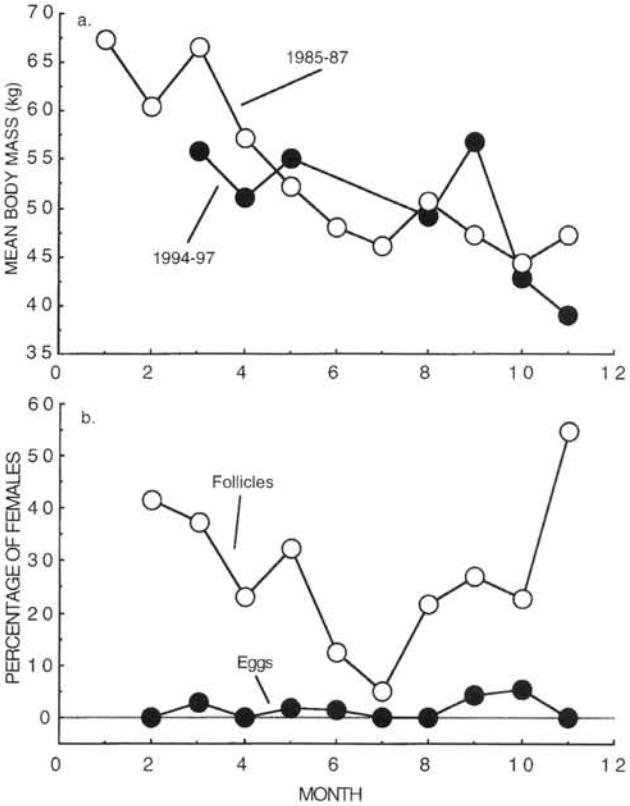

Figure 7. Monthly mean body mass of *E. imbricata* caught during 1985–87 (○) and 1994–97 (●) in Zone D (top, a). Percentage of female *E. imbricata* > 75 cm SCL sampled during 1985–86 that had enlarged follicles (●) and oviductal eggs (○) (bottom, b) (after Moncada et al., 1998a). 1 = January, 2 = February, etc.

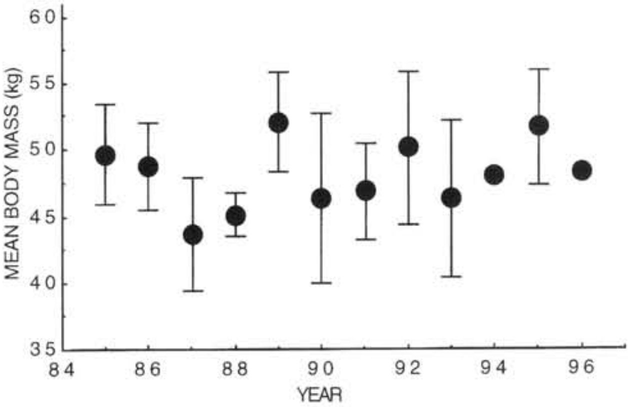

Figure 8. Mean body mass (± 2 SE) of *E. imbricata* caught in Zone D, 1985–96. Data are means of monthly means for August–October.

year when the percentage of females with enlarged follicles and eggs increased, but the peak time of nesting in Zone C is unknown. The seasonal cycles in size and reproduction were more similar to Zone B (ca. one month later) than Zone A (Moncada et al., 1998a).

Zone D. — This Zone contributed 27.5% to the historical Cuban harvest between 1983 and 1990. The main capture sites appear to be near coastal transit sites which include Nuevitas (Fig. 1), the second site in Cuba where harvesting occurs today. The *E. imbricata* caught in Zone D appear to be more mobile, and to come from other sites within and outside Cuba.

DNA samples from the current harvest in Zone D indicate 64% of sampled animals (38 of 59) have haplotypes from nesting areas in Zone A (Díaz-Fernández et al., 1999). There was a wider range of haplotypes in Zone D than in Zone A (14 vs. 9), and 10 (of 14) are shared with Zone B; 4 haplotypes from Zone D are not represented in any Zone A or B samples examined to date.

Tagging results (Moncada et al., 1998b) confirmed that some *E. imbricata* from Zone D traveled to Zone A and to other sites along the north coast of Cuba. Two *E. imbricata* tagged in the Bahamas (Bjorndal and Bolten, 1998; MIP, unpublished data) and one tagged in the U.S. Virgin Islands (MIP, unpublished data) were recently captured in Zone D.

One *E. imbricata* fitted with a satellite tracking transmitter at Nuevitas swam northeast into the open ocean and then returned to the central north coast of Cuba (ca. 450 km traveled; MIP, unpublished data).

No nesting sites within Zone D are known definitively and relatively few animals with oviductal eggs were caught in Zone D (Fig. 7b). A high proportion of females with enlarged follicles were found in Zone D in November, which corresponded with the peak of nesting in Zone A. A proportion of the reproductively active females in Zone D in November may nest in Zone A.

The sample data available for Zone D are extensive for 1985–87 but relatively incomplete for other years. They allow some trends for turtles caught in some months to be examined.

Marked seasonal variation in the mean size of *E. imbricata* caught in Zone D also occurs (Fig. 7a). Mean mass between January and March was high and corresponded with a high proportion of adult females containing enlarged follicles (Fig. 7b). After January–March, there was a steady decline in mean size of turtles caught (data are not available for December). The proportion of reproductively active animals in November was very high (Fig. 7b), despite the small mean size of animals caught (Fig. 7a).

For the seven months in which equivalent data for 1985–87 and 1994–97 are available (Fig. 7a), there has been no significant change in the mean mass of animals caught (paired t-test; t = 0.85, df = 6, $p = 0.42$).

For August–October sample data on the mean size of turtles caught are available for most months in most years between 1985 and 1996 (Fig. 8). Mean size fluctuated from year to year but showed no significant increase or decrease (linear regression, $r^2 = 0.04$, $p = 0.51$) over the 12 years of records.

For the months in which comparable data were available for females > 60 cm SCL (March, April, September, and October) the sample data indicate the proportion of adult-

Table 8. Monthly harvest (metric tons liveweight) of *E. imbricata* reported from Nuevitas (Zone D) between 1980 and 1993. Trends are linear regressions indicating slope over time and significance. * Indicates a significantly better fit with a polynomial, in which harvests declined and increased in later years (-/+), or vice versa (+/-). Closed seasons were altered in May 1988 (after Carrillo et al., 1998e).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1980	0.6	0.6	0.9	1.8	3.9	-	-	-	3.0	3.3	1.3	0.1	15.5
1981	0.5	1.1	0.5	2.7	2.4	0.7	-	-	5.3	3.6	1.1	1.4	19.3
1982	-	-	1.1	3.6	3.2	1.9	-	-	3.4	3.2	1.5	2.6	20.5
1983	-	0.2	1.2	1.9	2.1	0.6	-	-	5.7	3.3	0.9	5.2	21.1
1984	-	-	0.7	2.0	3.2	0.5	-	-	3.4	2.5	0.9	8.5	21.7
1985	-	-	0.8	2.0	1.9	4.2	4.0	2.0	2.5	1.7	0.4	-	19.5
1986	0.1	0.1	1.3	1.2	2.6	3.7	6.6	4.3	2.4	1.9	0.2	0.3	24.7
1987	-	0.4	0.5	1.1	2.4	0.3	-	-	3.7	3.1	0.9	-	12.4
1988	-	-	0.2	0.9	0.1	-	-	2.7	3.2	2.0	0.7	0.4	10.2
1989	-	0.4	1.2	1.1	0.5	-	-	4.7	3.0	-	-	-	10.9
1990	0.4	0.3	0.7	1.5	-	0.1	-	5.5	3.8	1.8	0.2	0.1	14.4
1991	-	0.2	1.3	1.3	0.5	0.1	-	4.2	3.2	3.1	1.3	-	15.2
1992	0.6	0.5	0.6	1.8	0.7	-	0.7	6.7	4.0	3.0	1.0	0.1	19.7
1993	-	0.7	0.1	1.2	0.4	0.1	0.2	5.4	3.9	2.9	-	-	14.9
	*	*						*				*	
Slope	-/+	-/+	-	-	-	-	-	+/-	-	-	-	+/-	-
r^2 .97	.35	.01	.42	.75	.14	.83	.52	.16	.28	.20	.30	.16	
p .03	.15	.70	.01	.0001	.25	.03	.08	.14	.05	.12	.34	.15	

Table 9. Variation in *E. imbricata* sex ratio (SR; proportion of females), as a function of Zone and period of capture. Data are from 1985–86, using animals greater than 60 cm SCL (after Carrillo et al., 1998e).

	Jan-Mar		Apr-Jun		Jul-Sep		Oct-Dec		Mean
	SR	*n*	SR	*n*	SR	*n*	SR	*n*	SR
Zone A	0.80	145	0.79	200	0.70	137	0.66	240	0.74
Zone B	0.82	59	0.85	163	0.87	249	0.80	128	0.84
Zone C	0.79	81	0.65	400	0.66	286	0.81	146	0.73
Zone D	0.63	34	0.83	208	0.85	308	0.82	34	0.78
Mean	0.76	4	0.78	4	0.77	4	0.77	4	0.77

sized females stabilized over time (Carrillo et al., 1998e). The 1987–90 ($n = 264$ females sampled; 50.0% > 75 cm SCL, 30.7% > 80 cm SCL) results mirrored those from 1991–95 ($n = 133$; 52.6% > 75 cm SCL, 31.6% > 80 cm SCL). However, the decline in the proportion of adult-sized females in samples between 1985-86 ($n = 118$; 71.2% > 75 cm SCL; 48.3% > 80 cm SCL) and 1987–95 combined, was highly significant for both > 75 cm SCL (contingency table; $\chi^2 = 15.2$; $p = 0.0001$) and > 80 cm SCL ($\chi^2 = 8.19$; $p = 0.0042$).

Changes in Abundance. — For Zone B, all *E. imbricata* caught at Cocodrilos (Fig. 1) were recorded and thus the data (Table 7) reflect the total catch, using similar catch equipment and effort, over the period 1983–97. The results indicate no significant reduction in abundance over this 15-year period. Nor has there been any significant increase in the catch correlated with the major increase in the nesting population of *E. imbricata* in Yucatan (Mexico) since 1990 (Meylan, 1997), even though some animals of Mexican origin are known to be caught at Cocodrilos. These conclusions are consistent with claims of traditional fishermen, with over 50 years experience at this site, that the rate of catch for *E. imbricata* has changed little in living memory. In contrast, the same fishermen report that the rate of catch for *C. caretta* has declined over the last 50 years.

For Zone D, monthly records of the total live weight of *E. imbricata* landed at Neuvitas were maintained from 1980 to 1993, when the number of harvest sites was reduced (Table 8). The results are consistent with there being no significant decline in abundance at this site over a 14-year period of harvesting.

Changes in Sex Ratio. — The sex ratios of *E. imbricata* caught in the larger samples examined in 1985–86 were heavily biased towards females and showed little variation between Zones (Table 9). The same trends were apparent in Zones in which nesting occurs (Zone A) and Zones where no nesting is known (Zone D), so it is unlikely to be a bias associated with capturing animals off nesting beaches. Similar female biases occur in Australia (Limpus, 1992) and they may reflect fundamentally skewed sex ratios from temperature-dependent sex determination (Mrosovsky et al., 1992; Mrosovsky, 1994). The significance of reported seasonal fluctuations in some Zones (Table 9) is unknown.

Within Zone A (Table 10), sex ratios between 1983 and 1993 fluctuated around a stable mean (0.84 ± 0.016) and showed no significant trend over time. In Zone B, sex ratio was also stable (0.82 ± 0.005) and showed no significant trend between 1983 and 1997. For Zone D, the mean sex ratio (0.81 ± 0.06) was also stable over time even though reported sex ratios in the 1990 and 1996 samples are well outside the normal range of values.

Table 10. Variation in the sex ratio (SR; proportion of females) as a function of year for *E. imbricata* from Zone A (January–August, December), Zone B (January, February, October–December) and Zone D (August–October). *n* = number of animals sexed. Years are lumped for Zones A and B to increase sample sizes.

Zone A			Zone B			Zone D		
Year	*n*	SR	Year	*n*	SR	Year	*n*	SR
1983-4	169	0.82	1983	138	0.83	1985	71	0.82
1985	324	0.81	1984	102	0.82	1986	105	0.90
1986	487	0.89	1985-6	202	0.82	1987	76	0.91
1987	619	0.79	1996-7	207	0.82	1988	97	0.84
1988	355	0.79				1989	77	0.88
1989	395	0.90				1990	133	0.53
1990	326	0.82				1991	73	0.97
1991	313	0.90				1992	50	1.00
1992-3	280	0.87				1993	70	0.94
						1994	18	0.94
						1995	42	0.76
						1996	43	0.30
						1997	180	0.69

DISCUSSION

Assessing Harvest Impacts. — If the *E. imbricata* population within the wider Caribbean was totally open and mixed randomly (Bowen et al., 1996), the trends reported from Cuban waters may provide an index of the population within the wider Caribbean during the period of harvest. If the levels of interchange within the Caribbean were more restricted and regionalized (Bass, 1997; CCMA 1998), this would not be so. That Zone-specific differences were so extreme within the Cuban harvest data suggests that the harvest in different Zones was not sampling one homogeneously distributed population, and that the impacts of the harvest are likely to have been more regionalized. But even here, there are limitations. The trends identified in the Zone-specific harvest data essentially describe "what" happened during the harvests and it is seldom possible to identify "why" it happened with confidence.

That harvesting can and has reduced wild populations of *E. imbricata* in most parts of the Caribbean (Meylan, 1997) is well established. But population declines do not necessarily mean that harvests are unsustainable. To discuss the impacts of the Cuban harvest, it needs to be placed in a general harvesting context (Walters, 1986; Caughley and Sinclair, 1994; Tucker, 1995; Chaloupka and Musik, 1996; Erdelen, 1998; Choquenot et al., 1998) with the following criteria.

1. An animal population at carrying capacity in a stable environment can be expected to fluctuate around a stable mean over time, with the population dynamics (rates of reproduction, mortality, immigration, and emigration) essentially balanced. The dynamics increasing the population cancel those decreasing it so that the population stabilizes.

2. To sustain any significant wild harvest a population at carrying capacity would need to be reduced below carrying capacity. When reduced and left to recover, the popula-

tion dynamics can be expected to change (if the habitat is intact); rates of recruitment will then generally exceed rates of loss (in contrast to the situation in a stable population) so that the population can start recovering back to the levels at carrying capacity.

3. If the rate at which a population can recover is matched to a level of harvest, the reduced population can theoretically sustain a harvest. The population will stabilize at a reduced level and have a size- and age-structure different from that of the original population.

4. If the harvest level is increased or decreased, the population may stabilize at new levels, but if increased beyond the maximum rate of the population to recover (exceeding maximum sustainable yield, MSY) the population will continue to decline and the size and age-structure remain unstable.

5. The real response of a population to harvesting, measured definitively in the field, can be expected to be quite different from that predicted from information gathered from a population not subject to harvesting (Walters, 1997; Parma, 1998).

When the Zone-specific Cuban harvests are seen from this perspective, we reach the following conclusions.

1. The original size and structure of the population at carrying capacity in the distant past is unknown.

2. The extent of the initial reduction in the population is unknown.

3. The initial reduction probably occurred over a long period of time at different rates in different parts of the range of the species (Meylan, 1997) such that a mosaic of reduced but recovering and declining subpopulations probably coexisted and interchanged at different times.

4. The level of reduction needed to maximize the potential rate of increase (MSY) of any population of hawksbills is unknown.

5. The level of stability achieved in the wild harvested population is the only index available from the Cuban harvest for assessing sustainability.

Changes in the Population Over Time. — That the Cuban harvest as a whole was sustained during the 1980s and 1990s with no major increase in fishing effort suggests some level of stability and sustainability had been achieved. If all measured population parameters had been declining precipitously throughout the period of monitoring, there would be little doubt that the harvest was unsustainable. But this is not what happened. Changes occurred gradually. The Zone-specific harvest results indicate some seasonal harvests were based on populations which appeared to stabilize over time in terms of the parameters examined. Others remained unstable, and it is unclear whether this would or would not have rectified itself given more time. For example:

1. In Zone D, on the north coast of Cuba, the mean size of turtles caught fluctuated seasonally but showed no significant increase or decrease over time. The proportions of adult-sized females in the harvest stabilized and the abundance of turtles seemed reasonably stable. The results do not reject the hypothesis of sustainable harvesting from whatever population is harvested in Zone D.

2. In Zone A, the mean size of turtles caught declined over time. The decline was restricted to the non-breeding parts of the year, when the harvest appears to have been centered on animals resident and/or in foraging areas. The proportion of adult-sized females at this time of year also declined. The results support the view that the rate of harvest was excessive and unsustainable in the long-term. It has now been stopped. However, the mean size of animals caught during the breeding season appeared stable, which does not reject the hypothesis of sustainability, from whatever population is harvested in Zone A at this time of year.

3. In Zone B, the mean size of turtles caught declined and then stabilized, which does not reject the hypothesis of sustainable harvesting. Whether the proportion of adult-sized females has also stabilized is unknown, but will eventually be determined by ongoing monitoring.

Clearly, a suite of other factors are involved in determining whether or not a harvest is sustainable in the long-term.

Links Between Mean Size and Reproduction. — The relationship between the mean size of *E. imbricata* caught in different months in different Zones and the levels of reproductive activity among adult females (1984–86) was similar in Zones B, C, and D, although offset from each other by 1–2 months. Larger animals were caught earlier in the year, when relatively high numbers of reproductively active animals were also present. This correlation was quite different from the situation in Zone A, where larger animals and the peak of reproductive activity occurred later in the year. An anomaly to these general trends was a peak of reproductively active animals in Zone D in November, when the mean size of animal caught is much reduced (Fig. 7). This peak correlates more closely with the cycle of reproductive activity (and the mean size of turtles caught) in Zone A (Fig. 3), and may reflect the harvest in Zone D in November of animals destined to nest in Zone A.

Turtles caught during the reproductive period were longer rather than just heavier, than those caught at other times of year. This suggests movements associated with reproduction are intimately involved in the seasonal cycles of mean sizes recorded, even in Zones where no nesting (and thus harvesting off nesting beaches) was possible. Furthermore, that the cycle of nesting in Zone A appears quite different from that in Zones B, C, and D, supports the possibility that Zone-specific harvests were not necessarily sampling one homogeneously distributed population. Zone-specific immigration and emigration events could be affected by a variety of factors other than reproduction (e.g., ocean currents, food, temperature), which could in turn influence seasonal cycles in the mean size of turtles caught.

Harvest Impacts on Nesting in Cuban Waters. — The impacts of Cuba's historical harvest on *E. imbricata* nesting in Cuban waters have probably been significant. Within Zones A, B, and C, nesting beaches are sites where *E. imbricata* are vulnerable to capture and it would seem likely that many were caught in such situations during the long period of historical harvesting. There is no doubt that the numbers of adult-sized females caught during the harvest in Zones A and B declined during the period of harvest. No information within living memory suggests *E. imbricata* in Cuba ever nested in the high densities Meylan (1997) cites for Chiriqui Beach, Panama, in the 1950s, but perhaps such situations did exist in Cuba in the distant past.

In the 1980s turtle fishermen from throughout Cuba were interviewed about known nesting sites. Zone A, and particularly the Doce Leguas Keys (Fig. 1), was identified as the main nesting area, which was consistent with the reproductive information obtained from the sampling program (Moncada et al., 1998a). Since 1988 MIP staff have visited isolated keys and beaches in Zone A, surveying new sites and revisiting sites identified in previous years (Moncada et al., 1998a, 1999). The nesting beaches are generally small and to date (mid-1998) 47 beaches on 26 separate keys or islands in Zone A have been identified as *E. imbricata* nesting sites (Moncada et al., 1999). The maximum number of nests found in any one year was 251 from 25 beaches in 1994. It is not yet possible to quantify trends in the extent of annual nesting over time in any area but monitoring trials were started in 1997–98 on 10 offshore island beaches. In 9 of the 10 beaches the numbers of nests decreased sharply relative to spot checks in previous years, but it is unclear whether this reflects real trends in nesting or disturbance biases (Moncada et al., 1999). More information is required before the current status of nesting (whether it is increasing, decreasing, or stable) can be quantified.

Other nesting sites on islands and keys are known from Zone B (Cayo San Felipe, Cayo Canarreos, Isle of Pines) and Zone C (Cayo Ines de Soto) (Moncada et al., 1998a, 1999), but the extent and time of nesting is only now being investigated; none are known to support extensive nesting. The full extent of nesting in Cuba is thought to be in the range of 1700–3400 nests annually (Moncada et al., 1999).

Harvest Impacts on Populations Outside Cuba. — The extent to which the Cuban harvest has impacted populations outside of Cuba is largely unknown. DNA analyses (Bass, 1997; CCMA, 1998; Díaz-Fernández et al., 1999) suggest a reasonably high percentage of *E. imbricata* caught in Cuban waters may originate from nests in Zone A within Cuba, but individual turtles may move widely prior to returning to Cuban waters to feed or nest. Indeed, turtles of Cuban origin perhaps contribute significantly to foraging populations outside Cuba (Bass, 1997; CCMA, 1998). Satellite tracking has now confirmed that some *E. imbricata* caught in Cuban waters move widely within the Caribbean. What remains unclear, as discussed previously, is the level and nature of the exchange. The extent to which it involves random mixing throughout the Caribbean (Bowen et al., 1996), or a more structured interchange where individuals from Cuban waters, or particular Zones in Cuba, are more likely to spend time in one area outside Cuba than another.

In the absence of such information, one can still pose the hypothesis that the Cuban historical harvest did impact seriously on regional populations and that it caused widespread population declines in other parts of the Caribbean. Relatively few long-term hawksbill monitoring programs were operating in the Caribbean during the 1980s, and the most extensive data are from Campeche and Yucatan in Mexico (data compiled and summarized by Meylan, 1997). The nesting population in both sites was clearly reduced relative to past levels, and was itself subject to intense local harvesting (Hernández et al., 1995). However, between 1980 and 1991 the density of *E. imbricata* nests in Yucatan remained stable (linear regression: $r^2 = 0.02$, $p = 0.68$) and that in Campeche increased ($r^2 = 0.53$, $p = 0.008$; Fig. 9).

The only other population monitored throughout the 1980s was at Tortuguero, Costa Rica, where relatively few *E. imbricata* nest. The numbers of nesting females (Meylan, 1997) ranged between 5 and 21 in the 1970s, and between 1980 and 1991 fluctuated between 1 and 10 but showed no consistent trend over time ($r^2 = 0.03$, $p = 0.60$). Nest monitoring at Mona Island, Puerto Rico (Meylan, 1997), was clearly reduced relative to the past, but stable between 1986 and 1990, the only period when comparable data are available ($r^2 = 0.73$, $p = 0.07$). At Buck Island, U.S. Virgin Islands, between 1987 and 1991 the number of nests increased ($r^2 = 0.87$, $p = 0.02$) and in Jumby Bay, Antigua, there was no significant trend between 1987 and 1991 ($r^2 = 0.007$, $p = 0.97$).

These results themselves do not establish stability, because mean age or size of nesting females may have been declining and various other changes could have been taking place. But they suggest that despite regional populations being reduced, and still being subject to local harvesting, some level of stability was present. They are inconsistent with the hypothesis that the historical Cuban harvest was causing widespread and ongoing regional declines, although it may well have been constraining recovery.

In 1992–94 (Fig. 2) the annual Cuban harvest was reduced from an estimated 4247 to 996 turtles per year, and since then, to less than 500 per year. Harvesting in Zone A, on the southern side of Cuba, ceased altogether in 1994.

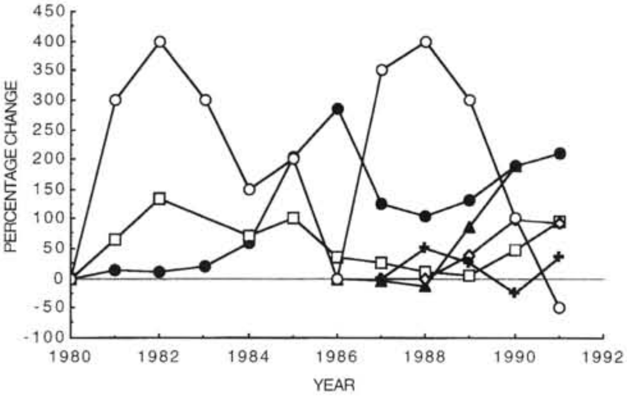

Figure 9. Percentage changes over time in reported monitoring results (nests, nesting females, nest density) at 6 widely distributed sites within the Caribbean between 1980 and 1991. Results are expressed relative to the first year ($N_1 = 0\%$) for which data are available (after Meylan, 1997). Campeche, Mexico (●), $N_1 = 1.58$ nests/km; Yucatan, Mexico (□), $N_1 = 2.85$ nests/km; Mona Island, Puerto Rico (▲), $N_1 = 68$ nests; Buck Island, U.S. Virgin Islands (◇), $N_1 = 63$ nests; Jumby Bay, Antigua (✚), $N_1 = 103$ nests; Tortuguero, Costa Rica (○), $N_1 = 2$ females.

Between 1992 and 1996, monitoring results from Buck Island, Jumby Bay, and Tortuguero (Meylan, 1997) showed no increase in the nesting populations correlated with the reduction in the Cuban harvest. In contrast, at Mona Island in 1994 and 1996 annual nest numbers were nearly double those recorded in the 1980s, and this may well be linked to the reduction of harvesting in Cuba.

In Campeche and Yucatan, the density of *E. imbricata* nesting has increased exponentially since 1988–89, which correlates statistically with the phasedown of the Cuban harvest. However, whether there is a cause and effect relationship is unclear. Mexico introduced a new and significant program for protecting all marine turtles and restricting local use and trade in 1990. With the possible exception of leatherbacks (*Dermochelys coriacea*), all marine turtle species in Mexico have responded to the improved management in a similar way (Hernández et al., 1995; Márquez et al., 1996), including those on the Pacific coast and olive ridleys (*Lepidochelys olivacea*) in particular, which have rarely been encountered in Cuban waters (Carrillo and Moncada, 1998). Improved management in Mexico, rather than the phasedown of Cuba's harvest, would seem to be the prime factor driving the recovery reported from Mexico.

If the Cuban historical harvest was constraining the rate of recovery of other regional populations in the Caribbean, then the voluntary phasedown of the harvest can and should be seen as a significant contribution to the improved regional status of hawksbills in the Caribbean.

Population Size During the 1980s and 1990s

A wild population of a certain size was needed to sustain the Cuban harvest, even if its boundaries are unknown. Analyses of the Cuban harvest data by Doi et al. (1992), Heppell et al. (1995), and Heppell and Crowder (1996), concluded that any such wild population must have been substantial. Estimates of 20,000 to 118,000 adult hawksbills (Heppell et al., 1995) means total non-hatchling populations of hundreds of thousands if not millions. From a regional perspective, these estimates would need to be expanded further to account for significant harvests occurring outside of Cuba.

One obvious problem with these estimates is that they are inconsistent with the numbers of nests known from Cuba and the wider Caribbean (Pritchard, 1997; Meylan, 1997; Moncada et al., 1999). This suggests that either the wild population estimates are too high, the estimates of nest numbers in the Caribbean too low, or the estimates of the proportion of females nesting are in error.

In deriving these population estimates it is assumed that the harvest in Cuba was sustainable: that the wild population supporting the harvest, although reduced, had stabilized. This creates an overestimating bias, because the data presented here indicate that as a whole it was not stable. However, neither was the population declining precipitously during the 1980s and 1990s, so this bias alone is unlikely to explain the disparity between the estimated population size and the known extent of nesting.

Carrillo et al. (1998b) questioned whether the other population parameters used to model the population were in error. Of particular importance, they suggested that the mean age of adult females in a population subject to prolonged harvesting would be reduced relative to that in a population at carrying capacity. This factor alone reduces the size of the wild population estimates (4000 adults, Carrillo et al., 1998b; later revised to 5865 adults, CCMA, 1998), and is considered more consistent with the modest extent of nesting in Cuba and the wider Caribbean (Meylan, 1997). It is also consistent with independent findings that the long-term harvesting of *E. imbricata* in the Solomon Islands resulted in nesting becoming increasingly restricted to younger, smaller adults (Groombridge and Luxmore, 1989).

The question as to how a population of 5865 adults (110,000 non-hatchlings) could sustain or even approach sustaining the historical Cuban is not theoretically complex. Carrillo et al. (1998b) used the same age-specific survival rates used by Doi et al. (1992), Heppell et al. (1995), and Heppell and Crowder (1996) for ages 1 onward (0.95 per year), and used growth rates to maturity (100% of females by 20 years; 50% by 15 years) consistent with independent regional estimates of growth rate (reviewed by Carrillo et al., 1998b, and intermediate between those used by Doi et al., 1992, Heppell et al., 1995, and Heppell and Crowder, 1996). Sustainability could theoretically be achieved if on average 2.8% of hatchlings survived to one year of age; a possibility within the bounds of biological feasibility.

In reality, the ability to accurately model any marine turtle population is severely constrained by poorly known population parameters, especially survival rates (Chaloupka and Musick, 1996; Carrillo et al., 1998b). The population supporting the Cuban harvest may have indeed been much greater than that suggested by Carrillo et al. (1998b). However, that it could be biologically feasible for a more modest wild population to sustain a significant harvest would seem an important possibility worthy of further study. As emphasized by Chaloupka and Musik (1996), even minor changes in survival rates can have profound effects on models simulating marine turtle population dynamics. Everything else being equal, an increase in hatchling survival rates from 1% to 2% represents a 100% increase in recruitment rates.

General Conclusions

Perhaps one of the most important features of Cuba's historical harvest relative to harvests in many other areas (Meylan, 1997) was that the extent and nature of the harvest was controlled. Even when economic pressures existed to increase exports of *E. imbricata* shell, Cuba did not increase its catch effort to meet that demand. Another possible important element was that Cuba's main nesting areas were located on offshore, largely uninhabited islands, where the potential for harvesting eggs, even though eventually prohibited, was greatly reduced.

The harvest model presented by Mortimer (1995) would not appear to be directly applicable to Cuba, in that it modeled a situation in which recruitment stopped and ongoing harvesting removed animals hatched years before until none existed. In the case of Cuba, nesting continued throughout the period of harvest (even though levels were probably reduced) and juveniles and subadults remained common in coral reef areas and were always a dominant feature of the harvest, especially in Zone A. That older animals, hatched years before, were in fact steadily removed by the harvest is to be expected and is supported by the harvest data: animals over 90 cm SCL became increasingly rare as time went on. Whether the removal of these animals enhances the ability of young females to nest earlier is unknown but possible.

Whether the historical harvest was sustainable or not cannot be answered with the available data. The population was no doubt greatly reduced prior to the period of monitoring discussed here, but this in itself does not indicate the harvest was unsustainable (Caughley and Sinclair, 1994). The population parameters measured during the ongoing harvest, from the reduced population, indicate reasonable levels of stability were achieved in some Zones in some seasons, but not in others. These data do not confirm that the harvest was sustainable, but neither do they reject sustainability, which would be the case if all measured parameters declined precipitously. At a finer level of resolution, stability in the nesting population (regardless of the degree of reduction) is important. Mean clutch size and mass was stable from the late 1980s onward (Moncada et al., 1998a, 1999), but trends in nesting remain unclear. From the perspective of the current management of *E. imbricata* in Cuba the question of historical sustainability may be of more academic than practical significance. The historical harvest was reduced by 90%, stopped completely in Zone A, and is now associated with much more precise monitoring, nest surveys, and ongoing research.

The Cuban harvest data also shed light on the relationship between population decline and risk of extinction. Concerns about hawksbills (Baillie and Groombridge, 1996; Marcovaldi, 1997) are based largely on the extent of the historical decline in the global population (more than 80%) and the known levels of harvest relative to the known extent of nesting (Pritchard, 1997).

The Cuban harvest data indicate that despite wild populations being reduced within and outside Cuba, quite possibly by more than 80%, and having low numbers of nests (relative to other species), they could still at least partially sustain a significant harvest for many years. Added to this, the results from Mexico demonstrate the capacity to recover is not compromised by long periods of harvest that resulted in major population declines. Thus while there seems no doubt that there are many serious conservation problems facing hawksbill turtles in many parts of the world (Meylan, 1997), and that they deserve and perhaps need a very high level of conservation action and regional cooperation, imminent global extinction *per se* may not be one of them. At the very least, the extent of historical population decline may not in itself be a good index of risk of extinction for this species.

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