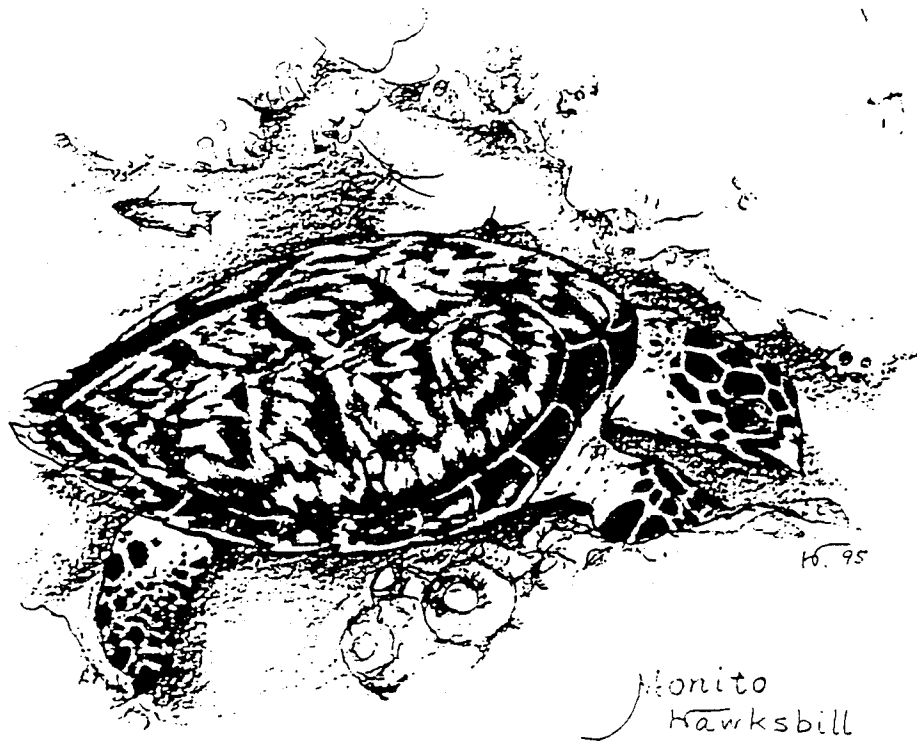


RESEARCH REPORT TO  
U.S. NATIONAL MARINE FISHERIES SERVICE

ECOLOGICAL AND POPULATIONAL ASPECTS OF  
HAWKSBILLS INHABITING THE NEARSHORE AREAS  
OF MONA AND MONITO ISLANDS, PUERTO RICO



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January 1996

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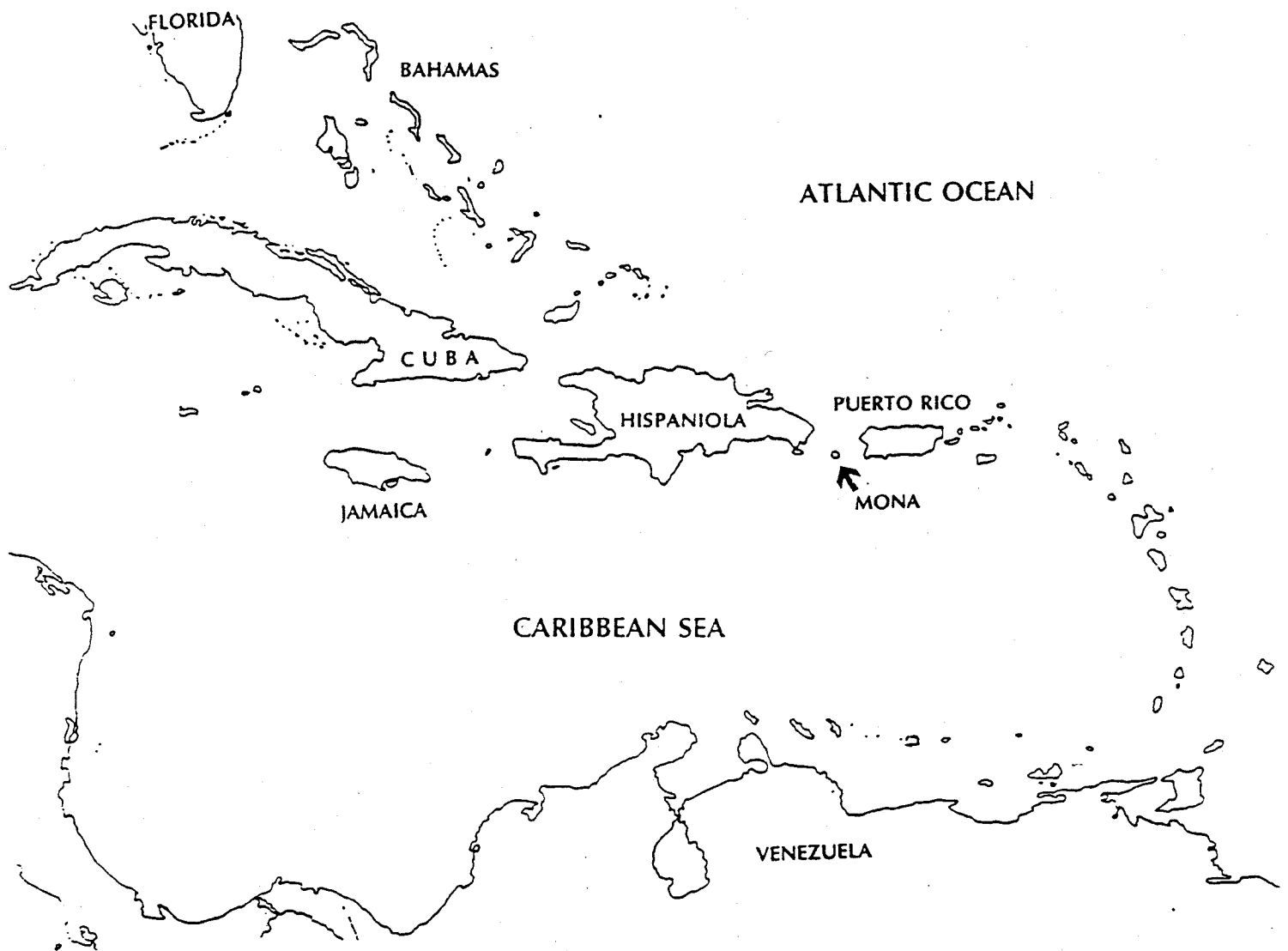


Figure 1. Location of Mona and Monito Islands in the Caribbean

## INTRODUCTION

In the summer of 1992 we started a pilot project to test the feasibility of a small scale, but comprehensive and long term study of the population dynamics and ecology of the hawksbill (Eretmochelys imbricata) at Mona Island, Puerto Rico. The use of various techniques for turtle capture, sampling and tagging were explored and methods suitable for working at Mona were developed and optimized. The population at Mona Island is one of the most important hawksbill populations remaining in the Caribbean. As Mona Island has such a relative abundance of individuals, with an excellent representation of the different size classes and offering good accessibility of the animals for research, it is now being recognized as a prime location for studying hawksbill ecology and population dynamics.

Current hawksbill conservation efforts are severely hindered by a lack of understanding of the basic biology of this endangered species. Our research is aimed at filling a number of these gaps. In particular, the work conducted in 1995 has yielded new information on hawksbill growth rates, diet, sex ratio's of immatures, and diving behavior. The methods used and data collected during 1995 on these topics, together with additional information, are presented in this report. Research results obtained previously are included whenever deemed appropriate and two submitted manuscripts concerned with hawksbill diving behavior are appended. More extensive analyses of the collected data are in progress and are being prepared for publication in peer reviewed, scientific journals.

## STUDY AREA

Field work during 1995 was carried out from July 11 to August 30 and again from December 14 to January 4, 1996, at Mona and its satellite, Monito Island. Mona Island (18°05'N, 67°54'W) is located in the Mona Passage between Puerto Rico and Hispaniola islands, and lies 72 kilometers West of Puerto Rico (see figure 1). The 55 km<sup>2</sup> island, a limestone platform rising to 100 m above sea level, features a coast of vertical cliffs along its northern half where water depth exceeds 30 meters. Towards the south, 6.2 kilometers of sandy beaches are fringed by a shallow reef system. Figure 2 shows Mona Island and the names and locations of the various sites referred to in this study.

Mona and Monito Islands are reserves managed by the Puerto Rico Department of Natural and Environmental Resources. Sea turtles have been formally protected there since the introduction of the Endangered Species Act of 1973. In 1982 the beaches of Mona Island were declared Critical Nesting Habitat for hawksbill turtles by the U.S. Fish and Wildlife Service.



MONITO ISLAND

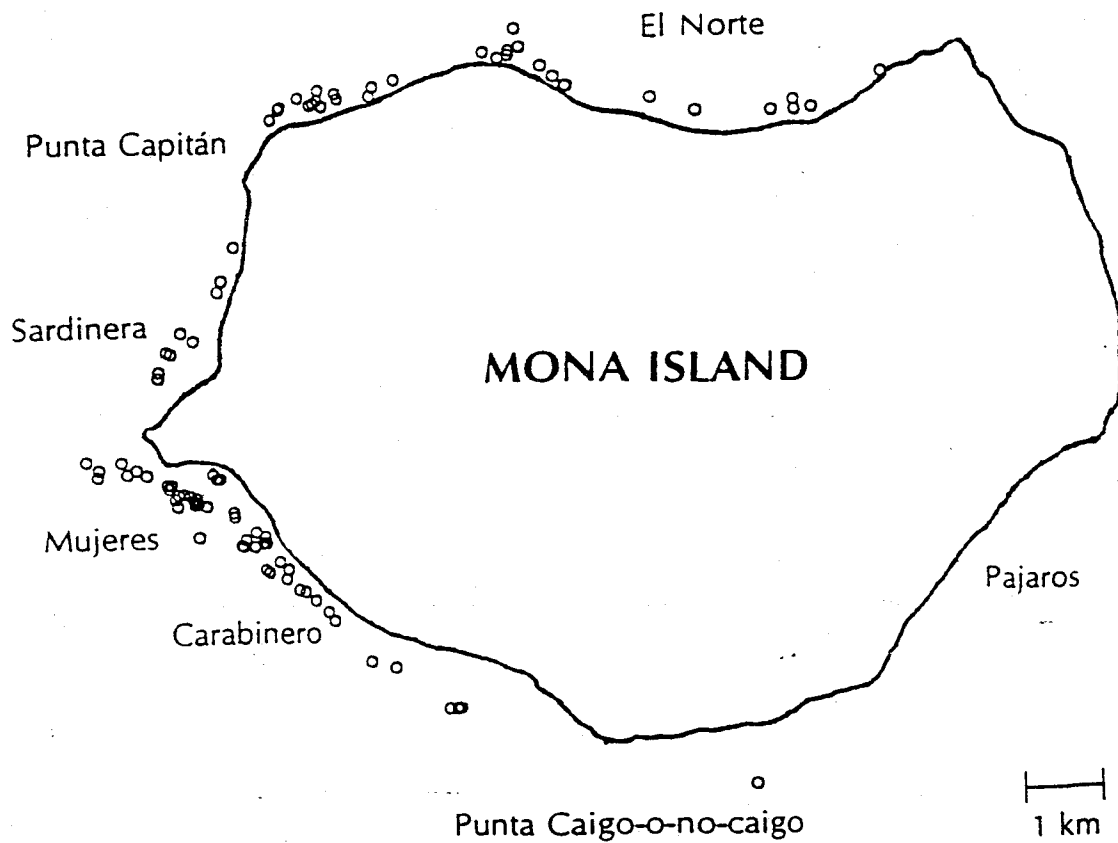


**Figure 2.** Mona and Monito Islands. Individual turtle capture locations are plotted as recorded by GPS receiver.

## METHODS AND RESULTS

### Turtle capture

Turtles were captured by hand in open water by snorkeling (skindiving) or with SCUBA. The 17 foot whaler "TAIMAI" fitted with a 40 horsepower outboard motor was used for most in-the-water activities and made for a reliable research vessel.

Surveys for turtles were made along the entire coast of Mona and Monito Islands. The methods used for these surveys consisted of snorkeling where water depth is less than 15 meters (50 feet), and a combination of snorkeling and diving with SCUBA or just diving with SCUBA, along the cliff coasts of Mona and Monito. Such surveys were made almost daily depending on weather and sea conditions. Good sea conditions are typically: clear water and little wind, waves or current.

The shallow water snorkeling surveys usually involved four people: three in the water and one person steering the boat. Those in the water swam in a certain direction, separating themselves to maximize area coverage, but remaining within visual contact of each other. A turtle sighting was hand-signalled to the others who then join in the pursuit of the turtle. One of two strategies was then employed: either one person would swim down towards the front or side of the animal to distract it while another person came from behind the turtle to grab it, or one person captured a turtle by swimming down from directly above the animal. Grabbing both its front flippers was found to be the most effective way of immobilizing and bringing up a turtle. Caution was used when doing this as some individuals try to bite the hands when handled in this way.

Along the cliff coast, where the vertical cliff wall stands in water between 20 and 40 meters deep, turtle capture was most effective when snorkelers and divers with SCUBA were present simultaneously. This method involved one or two divers swimming along the cliff wall at 10 to 15 meters depth, followed by one or two snorkelers at the surface. In this way, turtles seen swimming away along the cliff could be followed by the faster snorkelers, and turtles descending towards the seafloor could be pursued by the divers. Captured turtles were generally handled as described above, with the exception of very large animals captured by a single diver with SCUBA. In this situation, bringing the turtle to the surface could be accomplished by holding the turtle at the front nuchal notch and posterior end of the carapace and steering the animal towards the surface. When diver and turtle reach the surface, immediate assistance is necessary to prevent the animal from descending. During the 1995 field season, the majority of turtles were captured in the shallow reef areas extending from Carabinero to Mujeres and along the cliff face of El Norte and Monito Island.

Table 1a. Number of hawksbills captured and seen with effort expended in different study sites.

| Location             | Number of<br>turtles captured | Number of<br>turtles seen | Hours spent<br>in the water | Catch per unit effort<br>(turtle/hour) | Observed<br>(turtle/hour) |
|----------------------|-------------------------------|---------------------------|-----------------------------|----------------------------------------|---------------------------|
| Carabinero-Mujeres   | 52                            | 57                        | 47.18                       | 1.12                                   | 1.21                      |
| Sardinera-Carmelitas | 9                             | 8                         | 9.72                        | 0.92                                   | 1.17                      |
| Norte                | 31                            | 51                        | 19.09                       | 1.62                                   | 2.67                      |
| Monito               | 32                            | 52                        | 11.36                       | 2.82                                   | 4.58                      |
| Others               | 1                             | 7                         | 5.55                        | 0.18                                   | 1.26                      |

Table 1b. Number of green turtles captured and seen with effort expended in different study sites.

| Location             | Number of<br>turtles captured | Number of<br>turtles seen | Hours spent<br>in the water | Catch per unit effort<br>(turtle/hour) | Observed<br>(turtle/hour) |
|----------------------|-------------------------------|---------------------------|-----------------------------|----------------------------------------|---------------------------|
| Carabinero-Mujeres   | 5                             | 27                        | 47.18                       | 0.11                                   | 0.57                      |
| Sardinera-Carmelitas | 0                             | 4                         | 9.72                        | 0                                      | 0.41                      |
| Norte                | 2                             | 5                         | 19.09                       | 0.11                                   | 0.26                      |
| Monito               | 0                             | 0                         | 11.36                       | 0                                      | 0                         |
| Others               | 3                             | 4                         | 5.55                        | 0.54                                   | 0.91                      |

To determine capture location and make it possible to return captured turtles to the same site as where they were found, most capture locations were recorded using the Global Positioning System (GPS). A boatmounted Magellan Nav 5000D GPS receiver was used in two-dimensional mode to obtain capture location fixes. The errors involved with these GPS location fixes are generally less than 50 meters. Turtle capture locations for which GPS fixes were obtained are plotted in figure 2. Several immature and adult hawksbills were observed on the southeastern side of Mona, but turtles were difficult to catch in this high relief spur and groove filled reef area.

The effort involved with finding and capturing turtles at the three main study areas (the Carabinero-Mujeres and Sardinera-Carmelitas reef and the cliff walls of El Norte and Monito Island) was assessed by measuring the time spent for each survey session. Effort assessments were made for all survey sessions during the research period but does not include captures made incidentally. Surveys were generally performed with three people in the water. Tables 1a and 1b list the number of hawksbill and green turtles caught and seen (but not captured) and effort expended at each study site. With one survey hour defined as a unit of effort, the catch per unit effort (CPUE) is calculated for each study site.

During the 1995 research season, a total of 116 hawksbills and 11 green turtles were captured. Hawksbills ranged in size from 21.0 to 89.3 cm notch-tip straight carapace length (N-T SCL), green turtles ranged from 27.3 to 59.6 cm N-T SCL. Figure 3 depicts the size class distribution for both species.

#### Turtle tagging

All healthy turtles handled were tagged on both front flippers. Tags used were small Inconel, blue plastic tags, and PIT tags. Small Monel and Inconel tags were inserted using the tagging pliers in the second or third scute (counting from the base of the flipper) at the trailing edge of the left flipper, and on both flippers for turtles under 35cm straight carapace length (SCL). All applied tags were carefully checked for correct closure. Inconel tags in the SSL200 and SSM900 series were inscribed with "NMFS LAB, VIR. KEY, MIAMI FL 33149". Plastic tags in the BP4400 series read "REWARD PREMIO REMITE, SEND DEPT ZOOLOGY UF, GAINESVILLE FL USA". Only turtles larger than 35 cm N-T SCL were tagged using plastic tags and applied in the same position as metal tags, but by first making a 4 mm perforation through the scute with a disinfected leatherpunch and then using tagging pliers to insert the tag. Passive Integrated Transponders (PIT tags, TX1400L from Biosonics Inc, Seattle, WA, USA) were inserted to the muscle of the right front flipper. The advantage of these internal PIT tags is that even small turtles can be reliably tagged. PIT tag longevity in turtles is

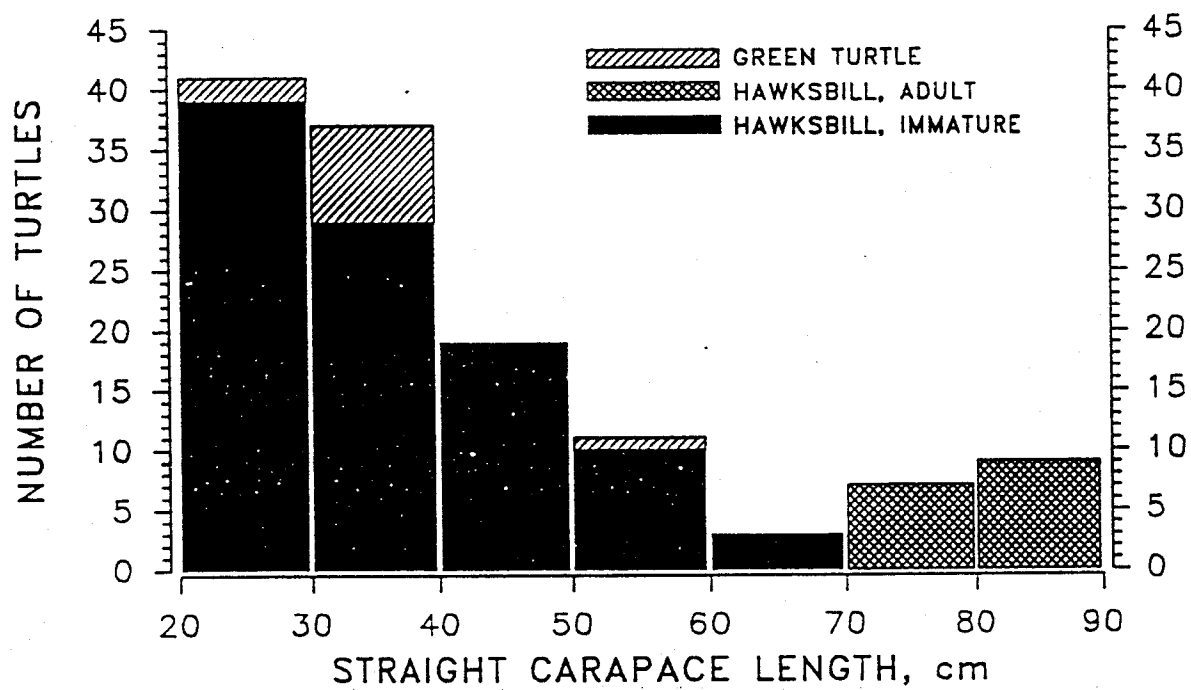


Figure 3. Size distribution of 116 hawksbills and 11 green turtles captured during 1995

estimated to be at least ten years. However, an electronic reading device has to be used to detect the tag and positively identify a turtle. Appendix I lists the tags of all turtles handled during 1995.

Of the 116 hawksbills captured during 1995, 67 were recaptures bearing tags applied during previous the field seasons on Mona. All eleven green turtles captured did not bear tags or tagging scars. No animals were found with tags not originating from Mona or Monito. From 1992 to 1995 a total of 232 turtles have been marked by us. PIT tags have been injected into 179 turtles, so far with an observed tag loss of 3.35% (6 tags); Monel tags were applied to 95 turtles, tag loss is 12.6% (12 tags); tag loss in Inconel tags is 1.78% (3 out of 168 lost); no tag loss has so far been detected for the 112 plastic tags applied.

### Biometrics

The following size measurements were taken of the turtles:

- straight carapace length (nuchal notch to posteriormost tip)
- curved carapace length (nuchal notch to posteriormost tip)
- straight carapace length (nuchal notch to posterior notch)
- curved carapace length (nuchal notch to posterior notch)
- straight maximum carapace length (anteriormost projection to posteriormost tip)
- curved maximum carapace length (anteriormost projection to posteriormost tip)
- straight maximum carapace width
- curved maximum carapace width
- straight plastron length
- curved plastron length
- straight maximum body depth
- straight maximum head width
- curved anterior vertebral scute width
- curved posterior vertebral scute width
- curved left anteriormost costal scute width
- curved right anteriormost costal scute width
- curved tail length plastron to cloaca
- curved tail length plastron to tail tip

Straight measurements under 40 cm were taken with 40 cm Haglof tree calipers, those over 40 cm with 127 cm Haglof tree calipers. Head width was measured with a vernier slide caliper. All readings were made to the nearest 0.1 cm. All curved measurements were made with one metric fiberglass tape measure, reading to the nearest 0.1 cm. Tape measure

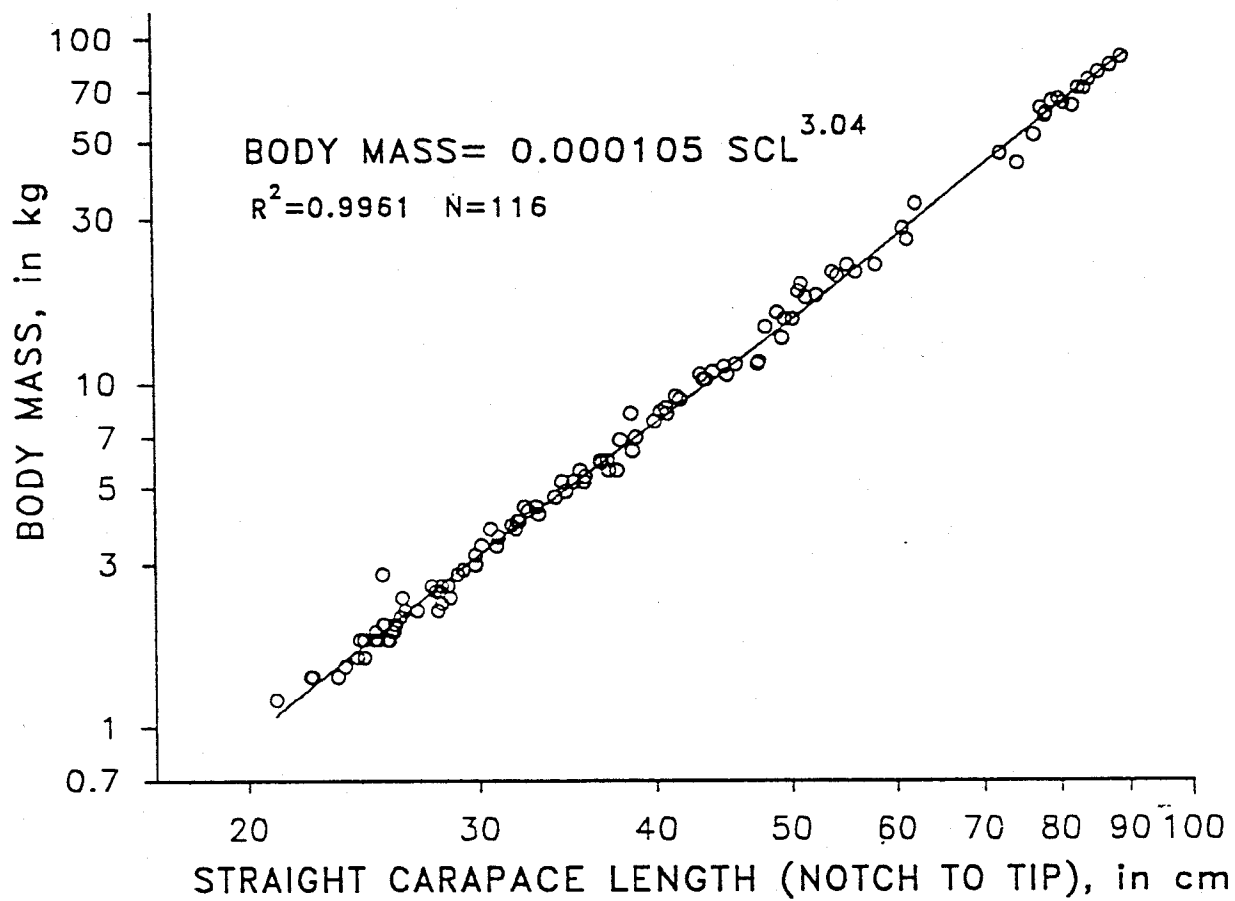


Figure 4. Relationship of turtle body mass versus carapace length

condition was checked regularly against the large tree caliper. Variation of two millimeters or less over the 120 cm span using typical tape tension was the criterion used for a sufficiently accurate and usable tape.

With length measurements involving the posteriormost tip of the carapace it was noted on which side the measurements were taken to insure consistency between measurements. In hawksbills, length of the left and right postmarginal scutes can vary considerably. To eliminate interobserver measurement error, all measurements and subsequent remeasurements of turtles were taken by the same person (CED or RvD).

Body mass measurement was made with Pesola spring scales (20kg x 200g, 50 kg x 1kg, 100kg x 1kg) and a Hanson Heavy Duty spring scale (90kg x 1 kg). Body mass measurements were made almost exclusively in a boat on the water, reducing measurement accuracy. Figure 5 illustrates the relation between body mass and straight carapace length (nuchal notch to posteriormost tip) obtained from the 116 hawksbills. A linear regression of the log-log transformed hawkbill mass-length data yields the following relationship:

$$\text{BODY MASS} = 0.000107 \cdot \text{LENGTH}^{3.04} \quad (N=116, R^2=0.9961)$$

Turtle length is straight carapace length (nuchal notch to posteriormost tip), in cm; body mass in kg. The regression line is plotted together with the individual data points on logarithmic scales in figure 4.

### Growth

Critical to understanding turtle population dynamics is knowledge of turtle growth rates, which in turn can form the basis of age to maturity estimates. Such data is largely lacking for hawksbills living under natural conditions. The tagging effort of the field work performed during 1992-95, aimed at juvenile and subadult hawksbills, provides a solid base for growth rates studies at Mona Island.

Sixty-seven hawksbills tagged in previous years were recaptured during 1995 yielded growth information. For comparative purposes, individual straight carapace length growth measurements were adjusted to yield growth values for an interval of one year (annualized growth). Annualized growth is plotted against N-T SCL (mean of previous and last measurement) for each of the four study areas examined (figures 5a,b,c,d). The figures include 39 growth measurements obtained prior to 1995.

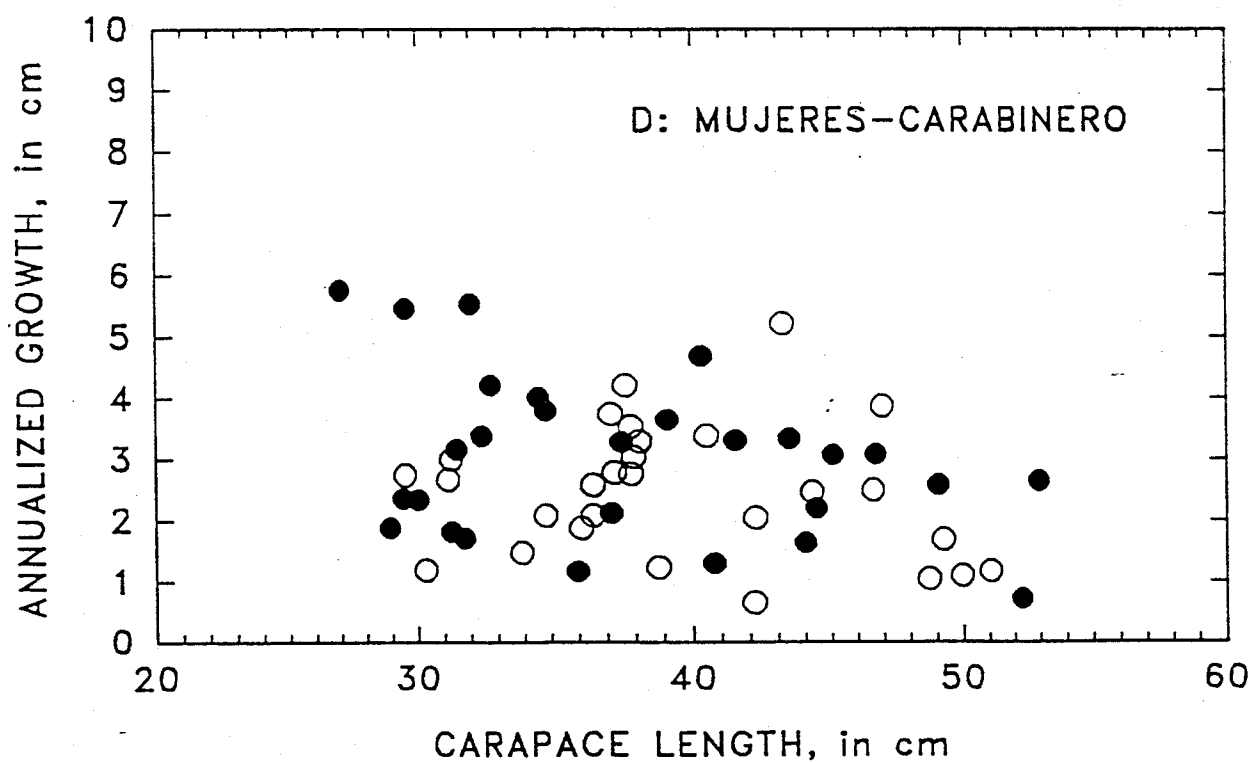
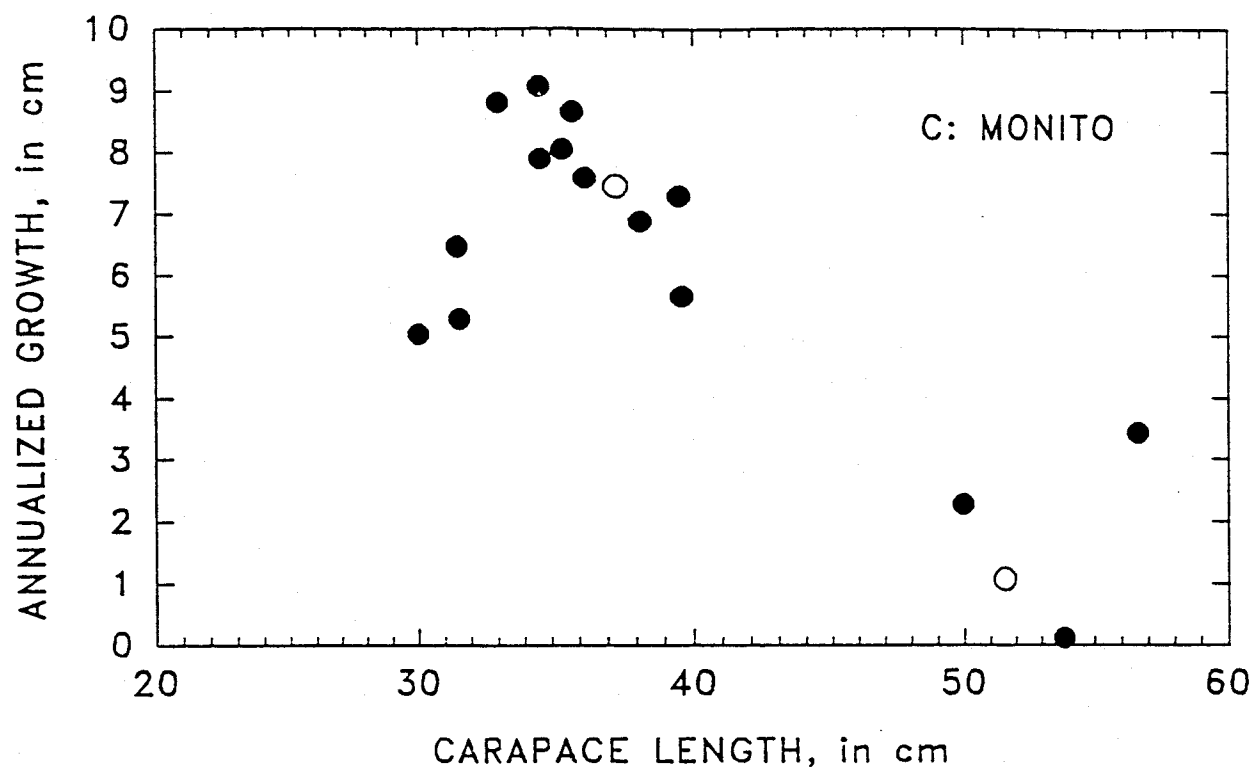


Figure 5. Hawksbill growth rates versus carapace length by study area.  
Open circles indicate data collected prior to 1995

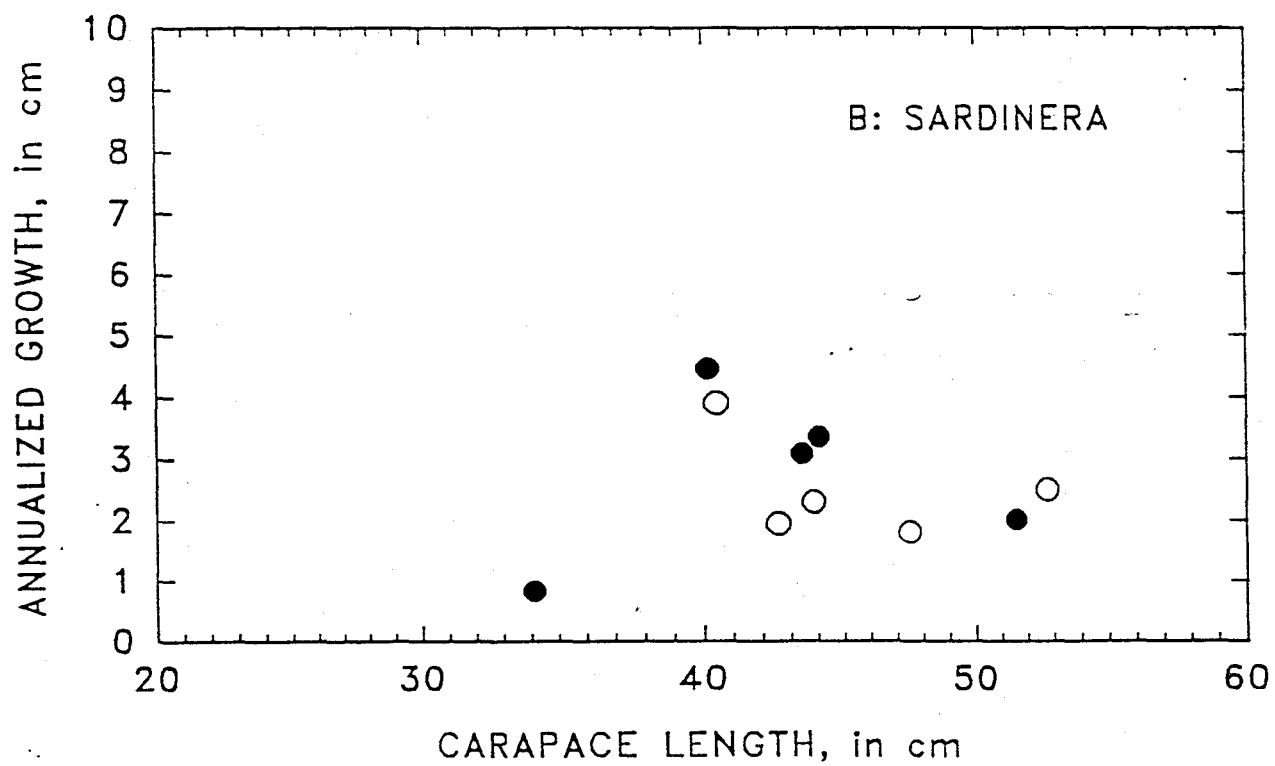
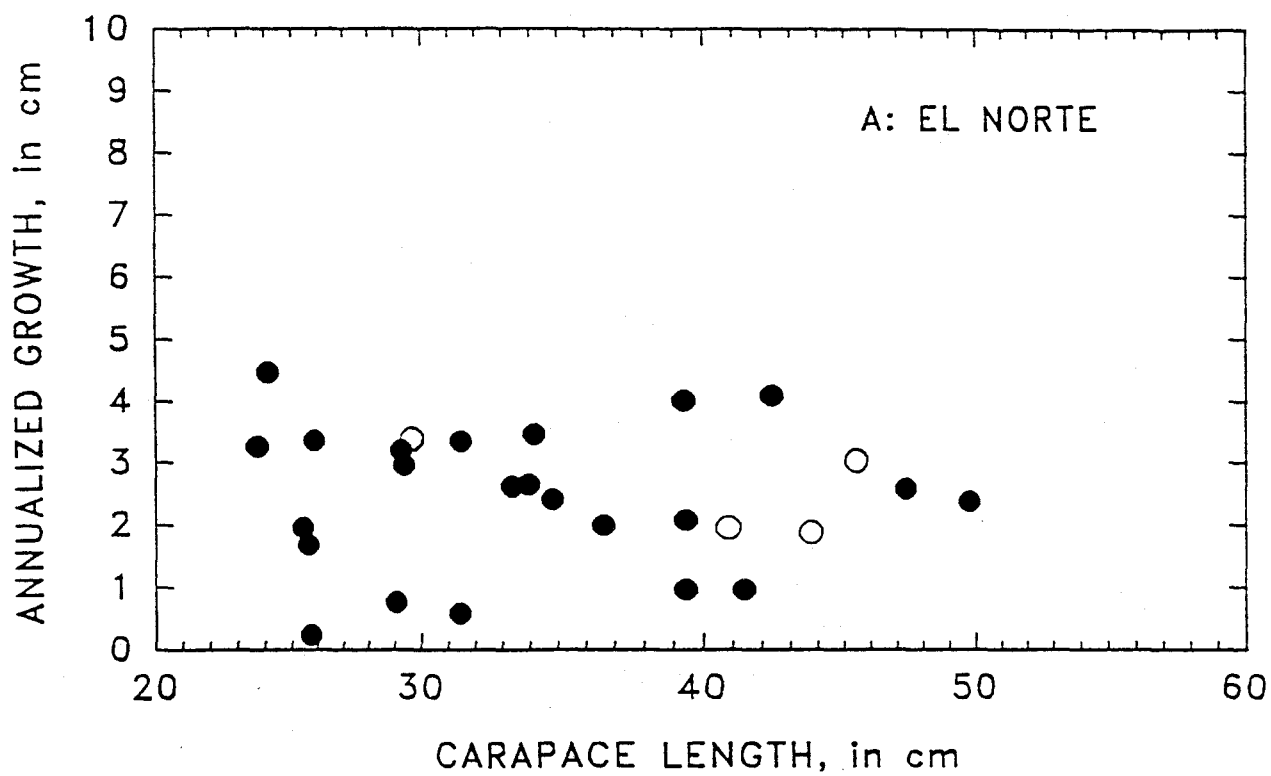


Table 2. Results of serum testosterone assays for 57 immature hawksbills collected at Mona Island, 1995.

|                   | Females | Males  | Unknown | Total |
|-------------------|---------|--------|---------|-------|
| Number of turtles | 30      | 24     | 3       | 57    |
| Ratio of total    | 52.60%  | 42.10% | 5.30%   |       |

## Turtle sexing

Measuring sex ratios of natural populations of sea turtles is essential to gaining an understanding of the population dynamics of these animals. The occurrence of biased sex ratios may have important conservation implications for wild sea turtle populations and their management.

Sea turtle population sex ratios may differ from 1:1 M:F for a number of reasons. First of all, it has been found that sea turtles exhibit temperature dependent sex determination; sex of an animal depends on the temperature at which it's egg was incubated. Secondly, mortality rates are likely to be different for females and males; nesting females are exposed to land predators, such as humans, while males do not return to ashore after entering the sea as hatchlings. Studies of sex ratios in a population should ideally include large numbers of turtles from a wide range of turtle size classes.

Immature turtles are not sexable by external characteristics. Even large, presumably adult turtles are known to have been wrongly sexed using criteria based upon tail length, etc. Currently, the only reliable techniques for determining sea turtle sex are measuring serum testosterone levels and through inspection of the gonads through laparoscopy. For our study we used both techniques to establish serum testosterone sex determining criteria for the Mona hawksbill population.

Blood samples were taken using Vacutainers with 22 gauge needles from the bilateral cervical sinus, a non-injurious technique. The volume of blood drawn from each turtle was approximately 10 ml. Whole blood was stored on ice prior to processing. Following centrifugation for five minutes, two 2 ml samples of blood serum per animal were extracted by pipet, labeled and placed in a freezer. During the subsequent transportation the serum samples were kept cold by placing them among solid carbondioxide (dry ice) pellets. The radioimmunoassay for determining serum testosterone levels was performed by staff of Dr David Owens' laboratory (Dept Biology, Texas A&M University).

Serum samples were collected and analyzed during 1995 for 57 immature hawksbills. The individual results of the hawksbill testosterone analyses can be found in appendix II. For immature Atlantic green turtles and Australian hawksbills, it has been found that a testosterone level of 10 pg/ml or lower is indicative of a female animal, and a level of 30 pg/ml or higher is typical of a male. One immature turtle, sexed as a female by laparoscopy had a serum testosterone level of 16.1 pg/ml and this level was adopted as the criterion for maximum level indicative of a female. The minimum male serum testosterone level was

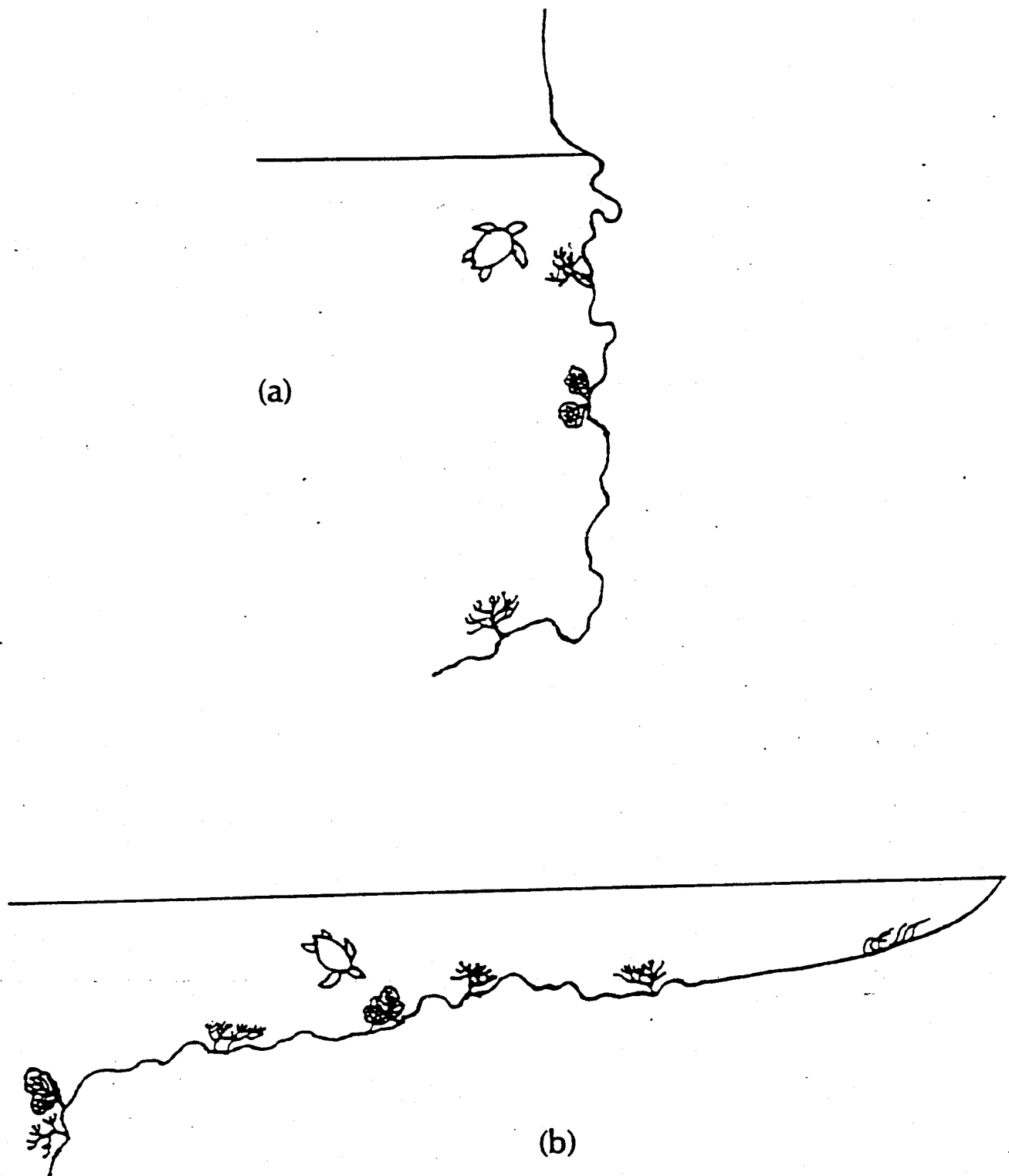


Figure 6. (a) Cross-sectional diagram of the cliff wall habitat at El Norte and Monito Island  
(b) Diagram of Sardinera-Carmelitas and Mujeres-Carabinero reef habitat

conservatively set at 30 pg/ml, resulting in three turtles sampled (with 18.9, 17.7 and 17.0 pg/ml testosterone) remaining unsexable. Table 3 shows the results of sexing during 1995 of the immature hawksbill population at Mona and Monito Islands. A light female bias (with 1.25 females to every male) was detected from these samples, which interestingly is in contrast with results obtained in previous years that showed a significant male bias in the immature hawksbill population.

### Foraging areas

Four areas were identified to be most important in 1995 for juvenile and hawksbill foraging: Carabinero-Mujeres, Sardinera-Carmelitas, El Norte and Monito Island. Other areas not studied around Mona Island but where hawksbills have been observed and likely represent important foraging areas are Playa Caigo, Coco and Brava, Punta Este.

The Carabinero-Mujeres area, where in 1995 we caught 45 hawksbills (39% of 116) and 6 green turtles (55% of 11) captured for this study, is characterized by a gently sloping seafloor (see figure 8b) that at Carabinero about 150 meters from shore and at 10 meter depth meets a vertical drop-off extending more than 50 meters deep. Towards Mujeres the edge of this drop-off is located further offshore and in deeper water. The shallow (up to 10 meters depth) terrace zone at Carabinero has a hard, flat bottom supporting an abundance of sponges and soft corals. Reef patches at Mujeres from 4 to 18 m depth are well developed, with typical structure heights of 1 to 2 m (up to 4 m) and overhangs and ledges providing turtles with ample shelter. Patches are covered with an assembly of macro-algae, hydrocorals, scleractinians, plexaurids, gorgonians, and the prominent encrusting sponge Anthosigmella varians. At Carabinero, a hard-bottom terrace is interrupted at 11 m depth, as close as 150 m from shore, by a vertical drop-off exceeding 75 m in depth. The narrow, almost flat terrace has extensive stands of Pseudopterogorgia sp. upon a substrate covered with Dictyota sp. and other macro-algae. Prominent sponges are Aplysina sp., Tethya sp., and Xestospongia muta.

At Sardinera-Carmelitas, where during 1995 we caught only 9 hawksbills (8% of 116), the study area consists of a forereef with spurs and grooves at between 5 and 12 m water depth, radiating outwards from a fringing/barrier reef. The reef spur structures seldom reach more than 1.5 m above the substrate. Beyond 12 m depth, about 400 m offshore, the system breaks up into large, sand-separated coral patches. Cover at 10 m depth is dominated by macro-algae, scleractinians, plexaurids and gorgonians.

Table 3. Occurrence of food items in samples collected in four study sites at Mona and Monito Islands (nf = item not present).

| Food item                        | Occurrence in % |          |           |         |
|----------------------------------|-----------------|----------|-----------|---------|
|                                  | Monito          | El Norte | Sardinera | Mujeres |
| Demospongiae                     |                 |          |           |         |
| <u>Geodia neptuni</u>            | 85              | 75       | 37        | 31      |
| <u>Polymastia tenax</u>          | 15              | 4        | 42        | 42      |
| <u>Stelletinopsis dominicana</u> | 8               | 17       | 11        | 11      |
| <u>Coelosphaera raphidifera</u>  | nf              | nf       | nf        | 23      |
| <u>Cinachyrella kuekenthali</u>  | nf              | nf       | 5         | 15      |
| <u>Chondrilla nucula</u>         | nf              | nf       | 21        | 8       |
| <u>Myriastru kallitetilla</u>    | nf              | nf       | 5         | 13      |
| Other                            | nf              | nf       | 16        | 9       |
| Algae                            | nf              | nf       | 16        | 9       |
| Miscellaneous                    | 8               | 4        | 5         | 2       |
| Unidentified                     | 8               | 8        | 5         | 15      |

Observations made at El Norte and Monito show that these cliff-side areas provide habitat to many hawksbills, from small juveniles to adults of both sexes. During 1995, we caught 34 hawksbills (29% of 116) and two green turtles along the cliffs of El Norte, while at Monito 26 hawksbills (22% of 116) were captured. Both areas feature walls extending down vertically to a depth of 25-40 meters where it meets a gently sloping, boulder strewn seafloor. The cave-strewn walls of the cliffs are heavily populated with an epifaunal assembly consisting of encrusting Porifera, calcareous and phaeophytic algae, and numerous other invertebrates. Niches and caves in the walls offer turtles both shelter and a foraging habitat. Hawksbills there tend to feed mainly off sponges growing on the cliff face along the upper 5 meter band extending from the surface down. During bad weather and whenever strong swells are present, hazardous conditions for both turtles and man prevail in this cliff wall area.

#### Esophagus/stomach and fecal content sampling and analysis

Lavage was used to sample food items for identification from the esophagus and stomach of a number of turtles. This non-injurious technique involved holding the turtle carapace down with the posterior end slightly elevated. No flipper restraints were used. The turtle's jaws were then gently pulled open using only the fingers. Once opened, a flat, stainless steel bar with rounded edges was inserted and held between the jaws. With the mouth held open, a flexible (vinyl or Tygon brand) tube of suitable diameter and lubricated with a light coat of vegetable oil was inserted into the esophagus. Tube sizes varied, from 8 to 20 mm outside diameter). All tubes had rounded ends to prevent damage to the esophagus while inserting. When the tube reached about 5-10 cm insertion, water flow through the tube was turned on and insertion was continued using a light backwards-and-forwards motion. Insertion length depended on the size of the turtle, from 20 cm for the smallest (approx. 25 cm SCL) to some 40 cm for the largest (50+ cm SCL) turtles sampled. Both piped water (ground water pumped to a cistern 15 m high) and a small hand pump were used as water sources. Water, together with food particles, was expelled through the mouth and collected in a clean bucket held beneath the turtle's head. Water flow was stopped after 1-2 minutes, the turtle was allowed to breathe, after which another 1 minute lavage was performed. With water still flowing, the tube was gently pulled free and the bar holding the mouth open removed. Next, the turtle was turned back onto its plastron and allowed to rest. The time necessary to complete the procedure seldom exceeded five minutes. Stomach samples containing sponges were fixed for 2 days in 8-10% formalin, after which they were washed with water and preserved on alcohol (70-80%). Algae samples were not transferred to alcohol, but kept in the buffered formalin solution.

Food sample identification was performed by us in the field. Each sample was drained, placed on a petri-dish, and sample constituents were sorted according to their gross external appearance. A preparation was made of each sponge sample by taking a small fragment (typically a few millimeters long) and dissolving it in 5% sodium hypochlorite (Clorox). After disintegration of the fragment (about five minutes), spicules were collected with an eye-dropper and placed on a microscope slide. Spicule preparations were studied using an Fisher binocular microscope with 4, 10, 40 and 100x magnification. Sketches of spicules found were made of each sample and comparisons were made with spicule sketches of samples identified during 1992 under the direction of Dr Vance P Vicente.

Sponge samples were identified to the lowest possible taxon, with the help of available literature. The sponge taxonomy adopted follows Van Soest. Sample wet weight (after having drained for several minutes) was measured to the milligram using an OHAUS bench scale at the U.S. Fish and Wildlife Caribbean Field Office.

A total of 70 esophagus/stomach samples were obtained during 1992 and 1993 through lavage from 64 turtles. Sample volume varied significantly from turtle to turtle. After lavage no signs of injury such as bleeding were observed in the turtles. Samples consisted almost entirely of sponges of the Class Demospongiae. Sponges were ranked according to frequency of occurrence and weight contribution by multiplying percentages of both. Table 4 summarizes our findings. Fifty-seven percent of samples were identified to belong to the following three orders: Astrophorida, Hadromerida and Poecilosclerida. The three most important sources of food for immature hawksbills at Mona Island Sponges were identified as sponges of the family Suberitidae, an Astrophorid sponge *Geodia* sp. (*Geodia neptuni*) and the sponge *Coelosphaera raphidifera*. *Coelosphaera* appeared only in turtles caught in the Mujeres-Carabinero area. However, we have not been able to recognize this sponge in the field and therefore it has not been possible to establish its distribution. For the Hadromerid sponge *Stelletinopsis* sp. the samples collected provide the first specimens recorded in Puerto Rican waters (pers. comm. V. Vicente).

In addition to the esophagus/stomach samples, fecal samples were collected after turtles produced them voluntarily. Samples were analyzed microscopically to determine principal constituents. Fecal components were mostly sponges and components generally followed those in table 4, although *Coelosphaera raphidifera* was not observed. Two unusual fecal samples were obtained from hawksbills caught at Cueva Esperanza-Cueva Espinal. The samples contained numerous smooth goose-necked barnacles (*Lepas anatifera*) attached to wood fragments. The turtles involved were small juveniles, one with N-T SCL of 27.6 cm, the other measuring only 20.0 cm. These findings suggests that the turtles had been foraging in the floating debris, a common occurrence where the turtles were found. Such feeding

may be similar to that of pelagic post-hatchlings and is indicative of possible recent arrival by these turtles from the open ocean environment.

### Diving behavior

Information on diving behavior was obtained for a total of eleven immature hawksbills by using time-depth recorders (TDRs) during 1994 and 1995. TDR work in 1994 focussed on turtles residing in the Carabinero-Mujeres, Sardinera and El Norte areas and results are presented in two manuscripts included here as Appendices III and IV. During 1995 we deployed two TDRs on turtles at Monito. The 7 x 4 x 1 cm recorders (model Mark V, Wildlife Computers, Redmond WA 98052) were affixed together with a sonic tag (model CHP-L, Sonotronics, Tucson AZ 85714) to the turtle carapace using epoxy adhesive. The digital TDRs were designed to sample and record ambient water pressure (corresponding with depth) every 8 seconds for the duration of 12.1 days. TDRs had a water depth resolution of 0.5 m and maximum registerable depth of 250 m. An underwater acoustic locator receiver (model N15A235B, Dukane Corp, St. Charles IL) was used to find the TDR and sonic equipped turtles both from the boat and in the water.

The complete dive records obtained for the two hawksbills at Monito Island are presented in figures 7a,b. Turtle 94-108 measured 43.3 cm N-T SCL, was released on December 19, 1995 and recaptured December 30. Turtle 95-122 measured 55.3 cm N-T SCL, was released on December 21, 1995 and also recaptured December 30. Both animals were recaptured within 500 m of the release location. The hawksbills exhibited distinct day and night-time diving behavior. From dusk until dawn (approximately 18:00 to 07:00 hrs) the turtles made 30 to 60 min dives to depths of 5 to 10 m. Minimal depth variation during these dives suggest that the animals were resting. Resting turtles show a remarkable tendency to return to the same depth after each trip to the surface to breathe, possibly to a fixed resting spot. Daytime dives were either shorter or deeper than dives made at night. Short and shallow dives with continuous variation in diving depth are likely to reflect prey searching and feeding behavior, such dives were made primarily in the early morning and late afternoon. Both turtles regularly made deep (30 to 40 m depth) and long (40 to 60 min) dives during the daytime. The purpose of these dives remains unclear, however several such dives may reflect resting behavior.

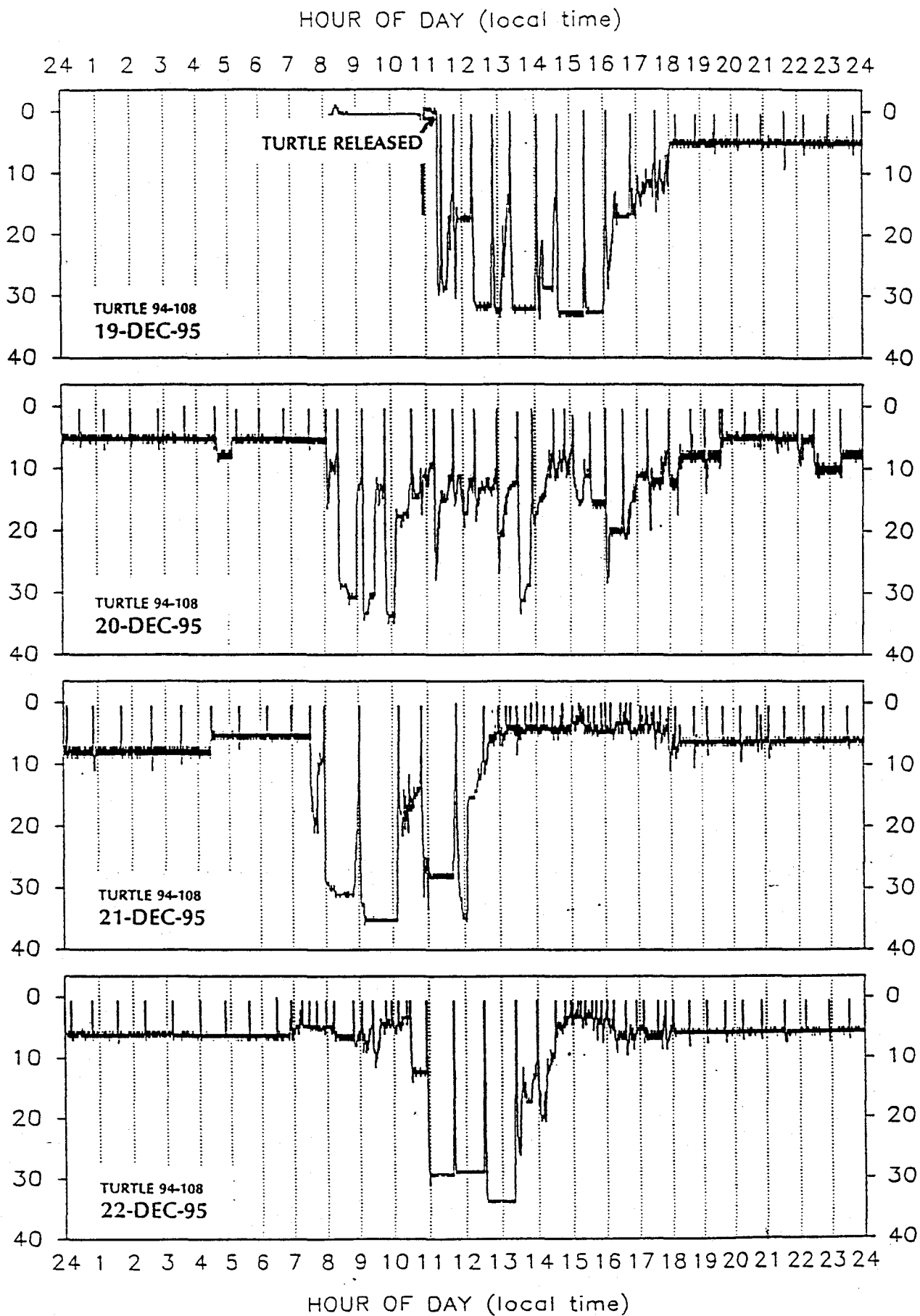


Figure 7a. Diving behavior of 43.3 cm N-T SCL hawksbill at Monito Island.  
Vertical axis is depth in meters

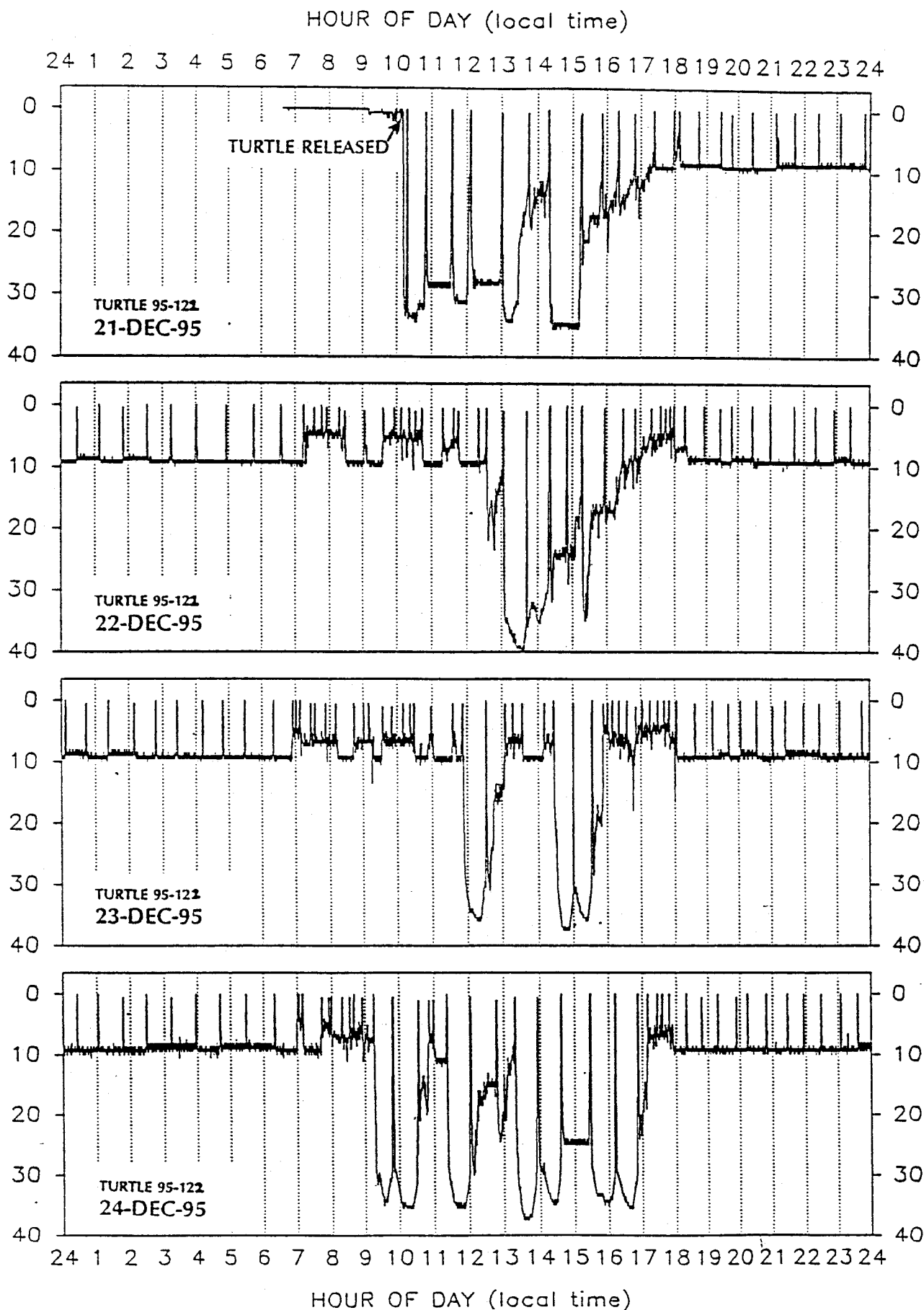
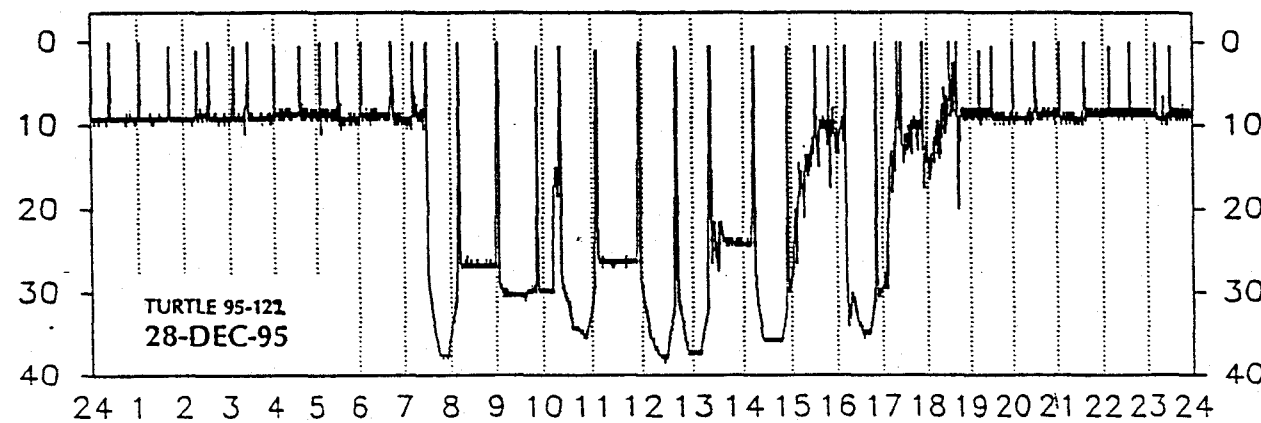
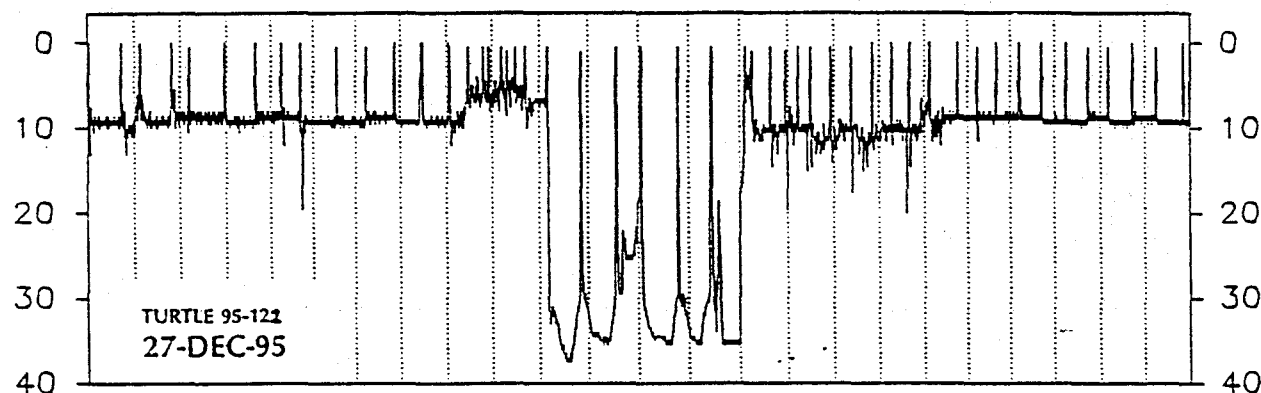
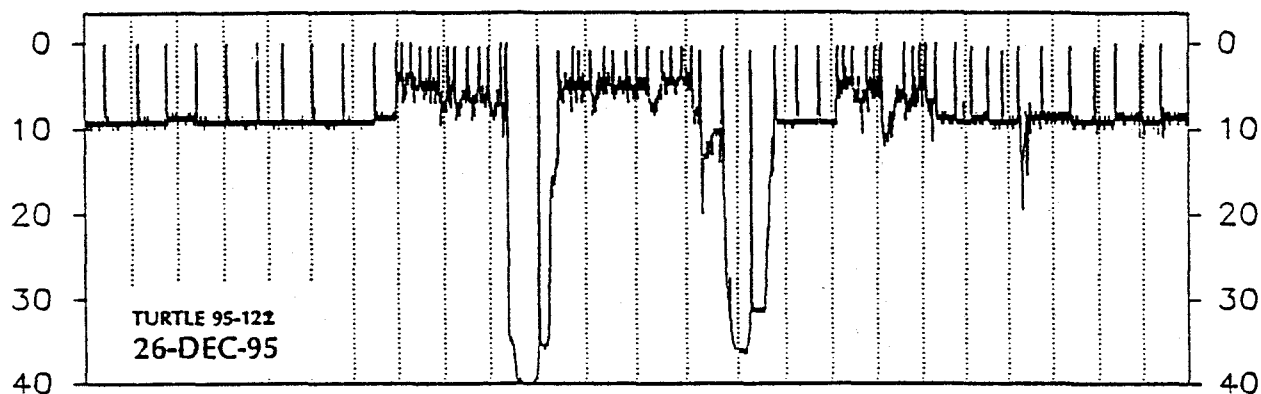
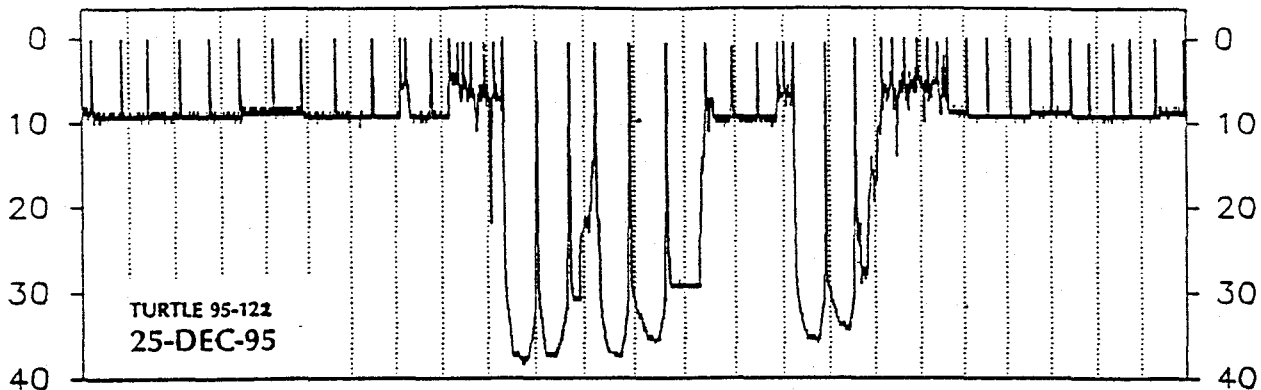


Figure 7b. Diving behavior of 55.3 cm N-T SCL hawksbill at Monito Island.  
Vertical axis is depth in meters

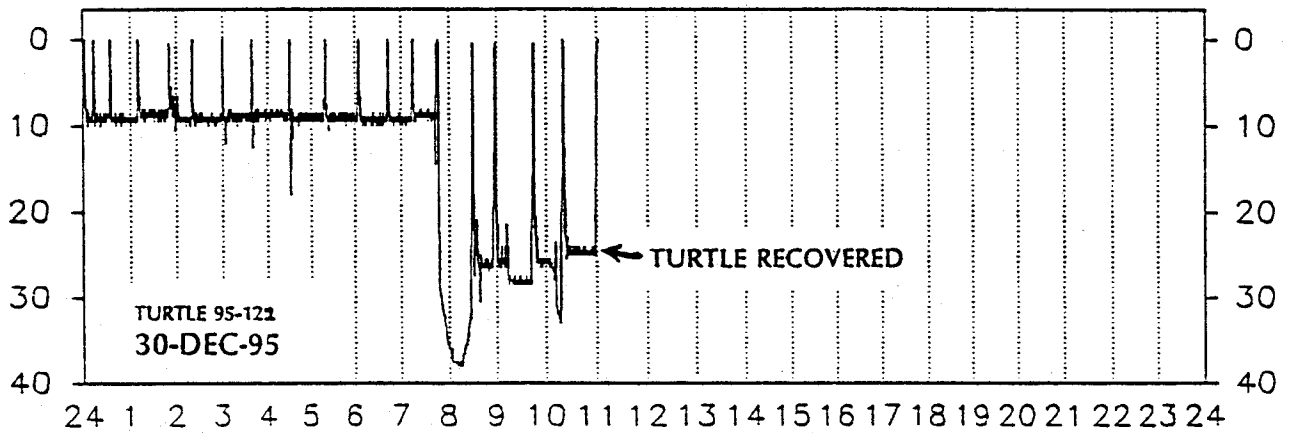
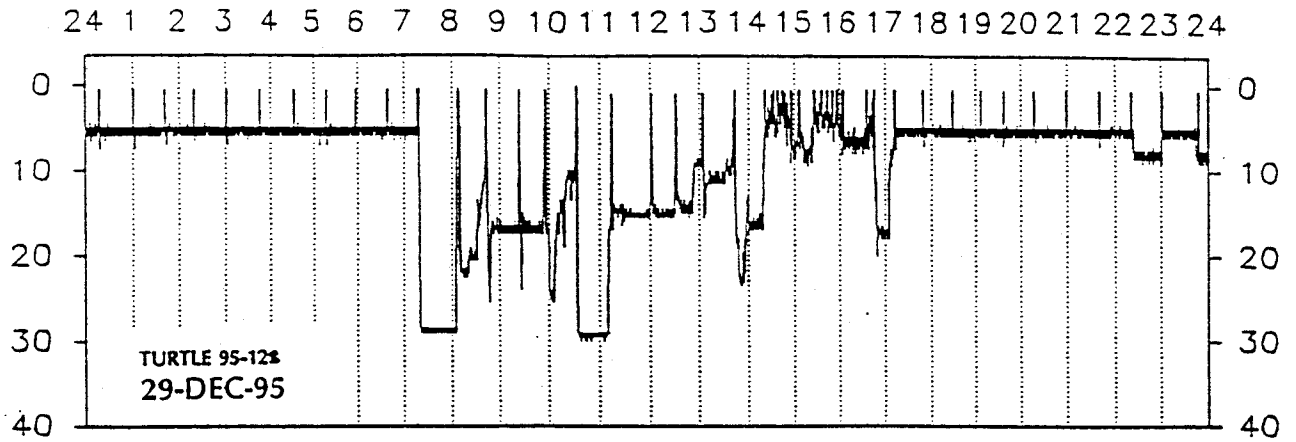
# HOUR OF DAY (local time)

24 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24



HOUR OF DAY (local time)

HOUR OF DAY (local time)



HOUR OF DAY (local time)

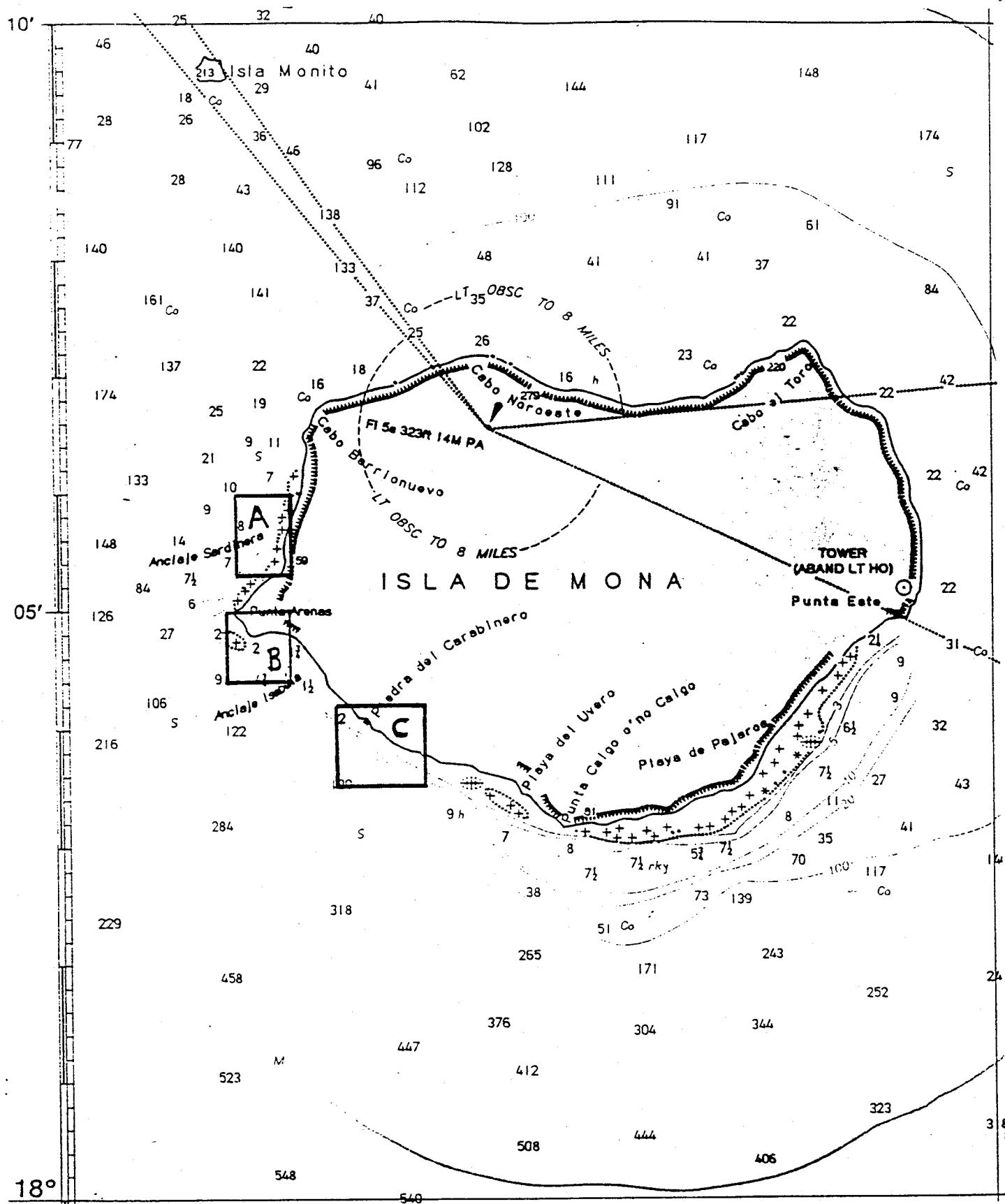


Figure 8. Immature hawksbill sonic tracking areas: A Sardinera, B Mujeres, C Carabinero

### Home range

Short term and long term movements of immature hawksbills was evaluated by sonic tracking and by comparison of capture/recapture locations. Locations were determined from by GPS receiver and reference to landmarks of known position. During 1995 sonic tags were applied for a three week period to three immature hawksbills at Sardinera, Mujeres and Carabinero (figure 8). The location of each turtle was determined every few days (figures 9a, 10a, 11a) and movement was examined in detail during one 12 hour daytime period (figures 9b, 10b, 11b). Movements of the Sardinera and Mujeres reef area turtles ranged from 500 to 800 m in extension. The Carabinero turtle moved within a longer (1 to 1.5 km) but narrow (100 to 300m) band of reef terrace.

Capture/recapture locations may be used to determine long term movement of hawksbills in their Mona and Monito habitats. Figure 12 shows the distribution of distances between 203 capture/recaptures locations. Figure 13 shows the same data but against time between capture. One small juvenile hawksbill moved from Monito to the El Norte cliff wall, a distance of 5.22 km. No significant correlation exists between distance traveled and time between capture (Pearson product moment,  $R^2=0.0182$ ,  $p=0.546$ ) suggesting the turtles do not gradually shift from one location to the next. Hawksbills appear to reside at Mona and Monito Islands for periods of at least several years. To date no tagged immature or adult turtle tagged at Mona or Monito has been reported from any other location.

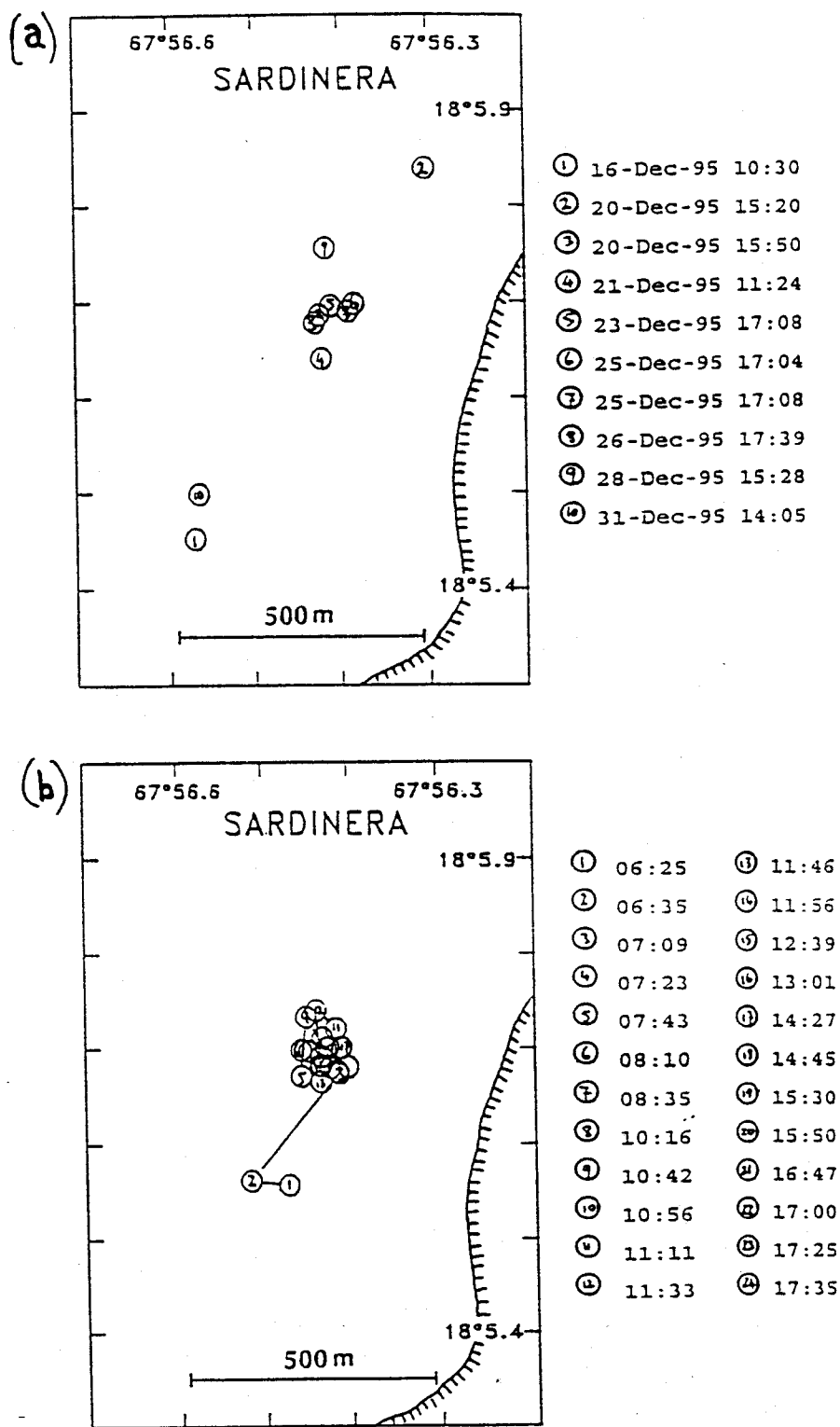


Figure 9. (a) Location of the 47.5 cm N-T SCL hawksbill 92-025 during a 16 day period  
(b) Movements of turtle 92-025 on 24-DEC-95

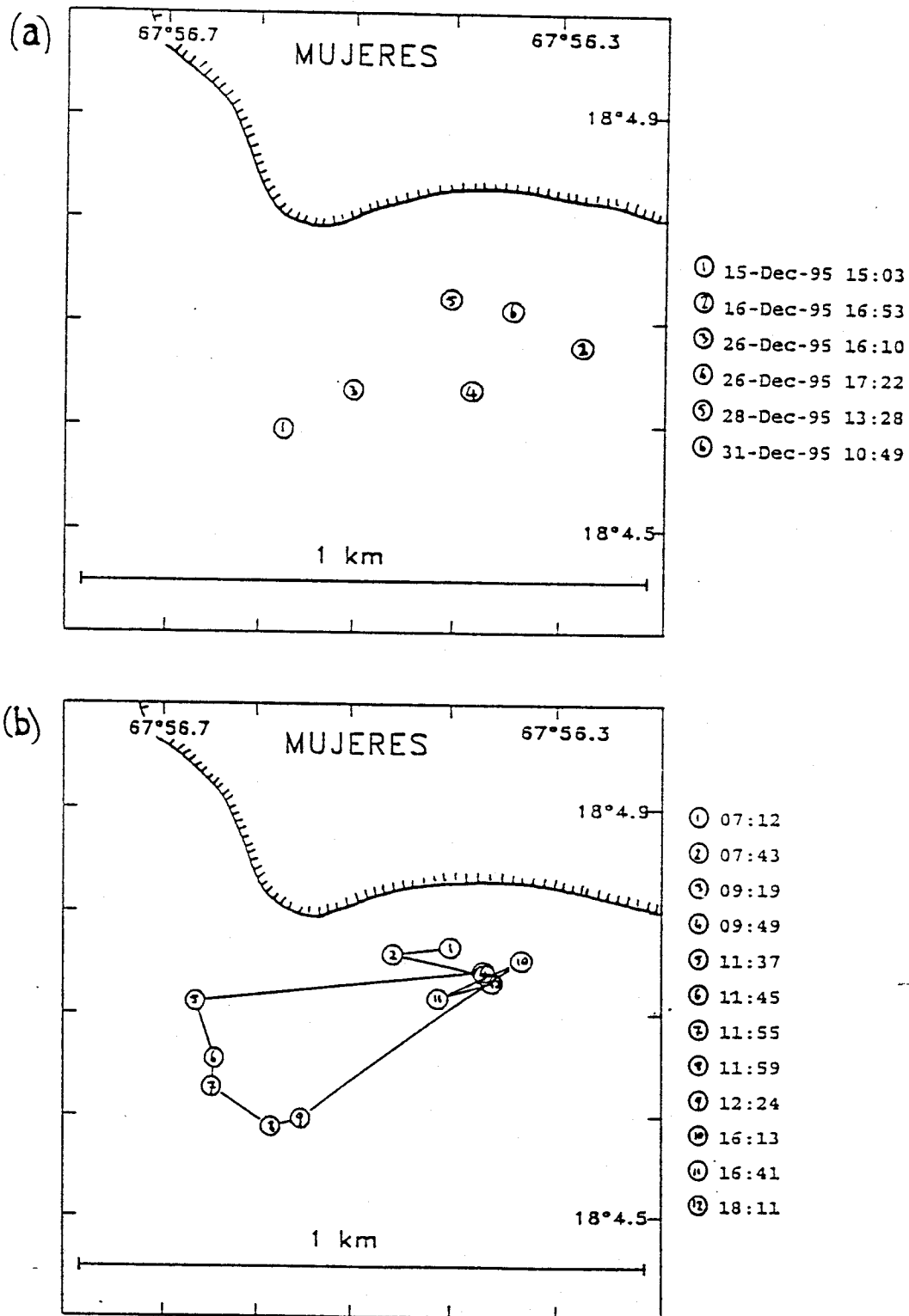


Figure 10 (a) Location of the 35.7 cm N-T SCL hawksbill 94-064 during a 17 day period  
 (b) Movements of turtle 94-064 on 22-DEC-95

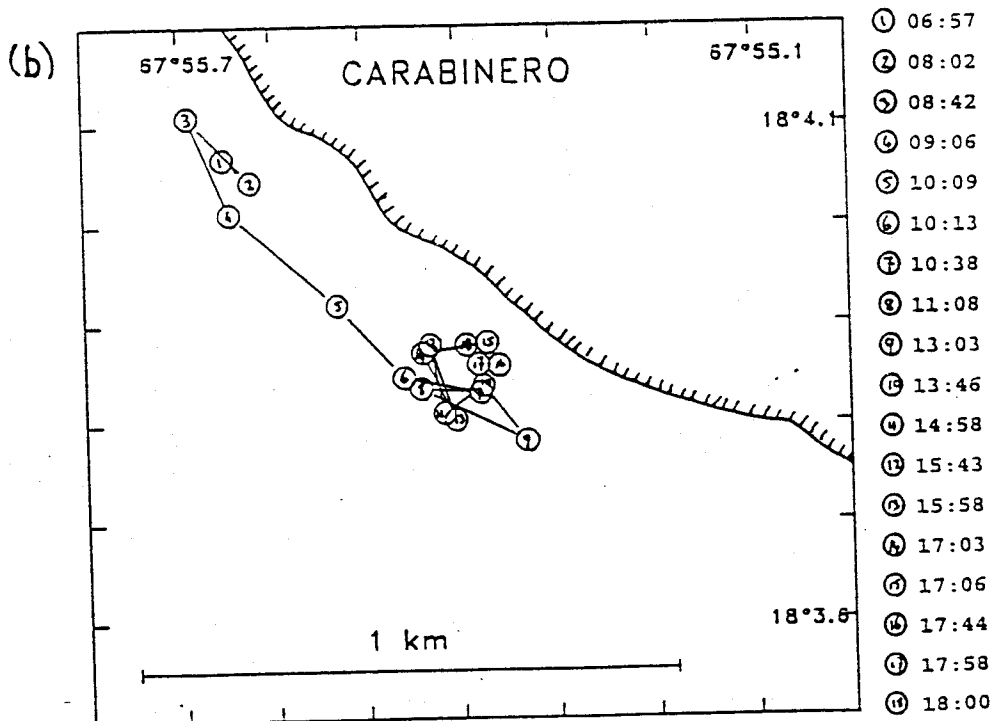
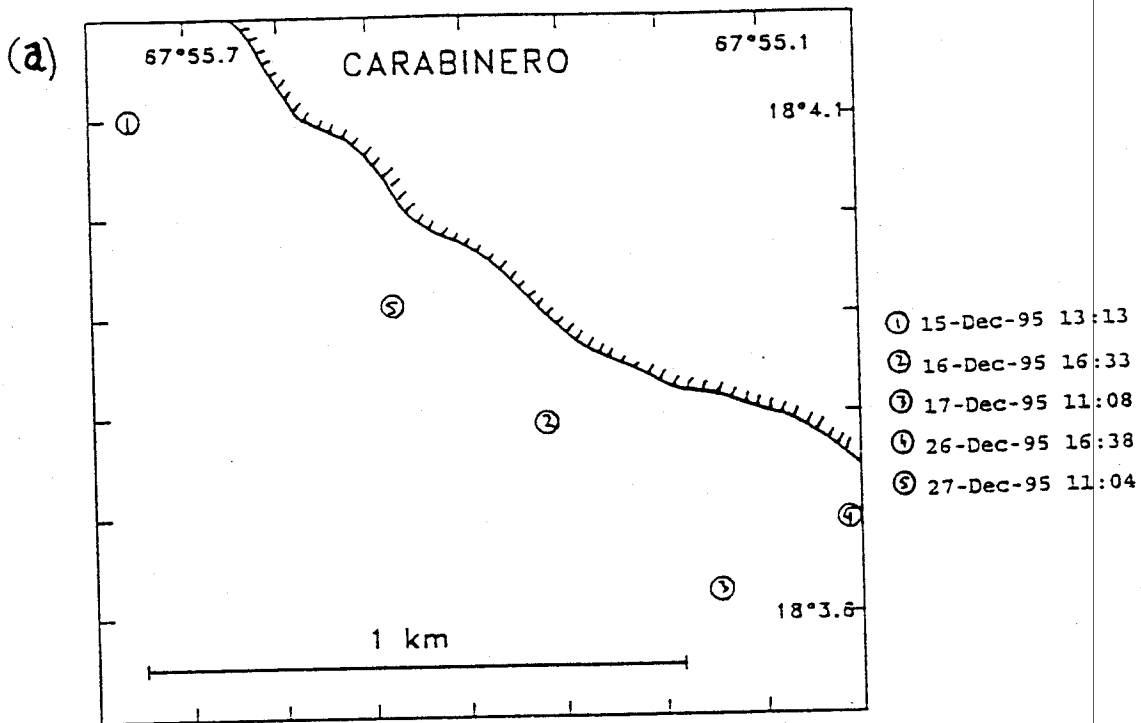


Figure 11 (a) Location of the 43.5. cm N-T SCL hawksbill 94-031 during a 13 day period  
 (b) Movements of turtle 94-031 on 22-DEC-95

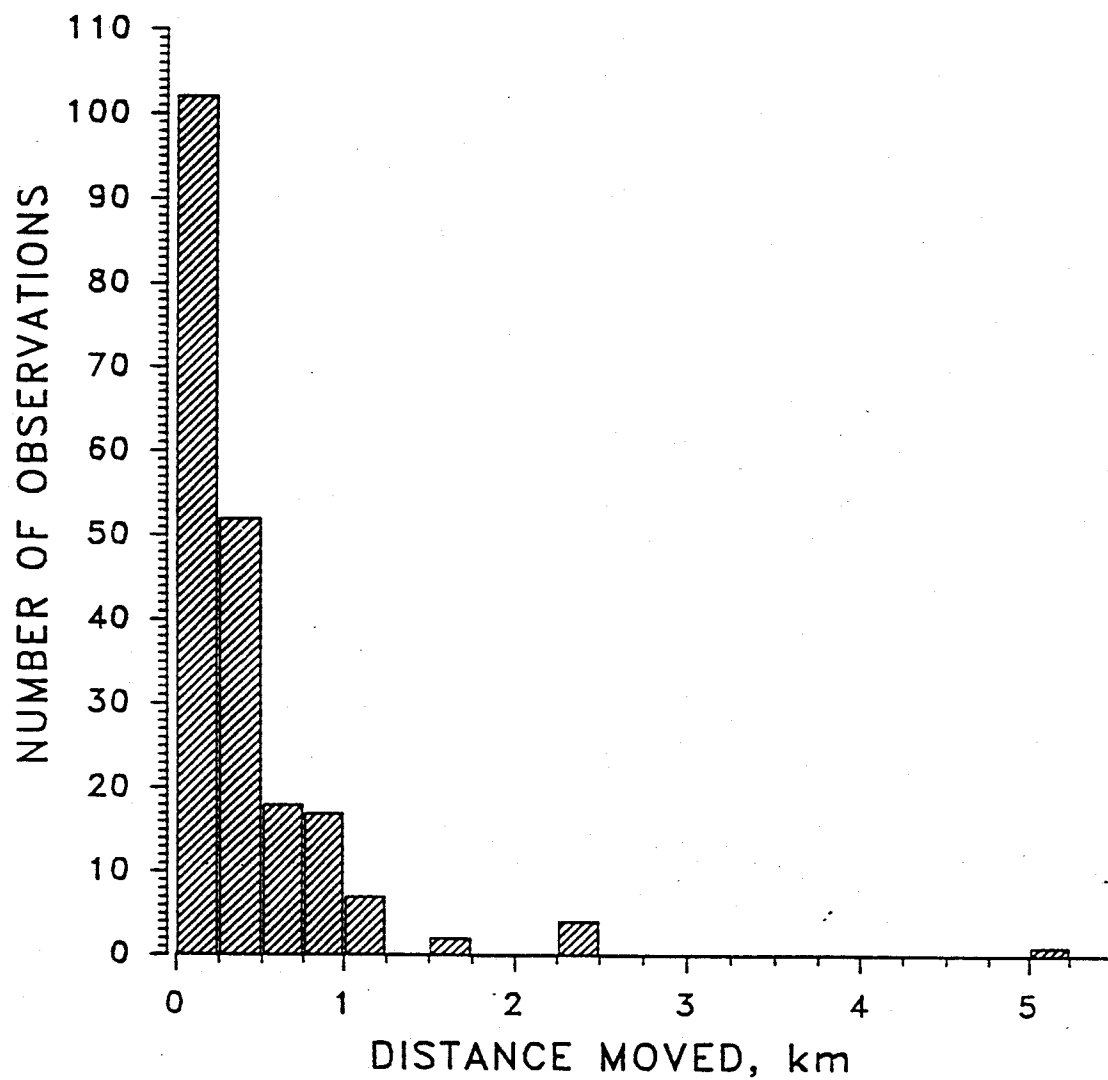


**Figure 12** Distribution of straight line distances moved between 203 pairs of immature hawksbill capture and recapture observations

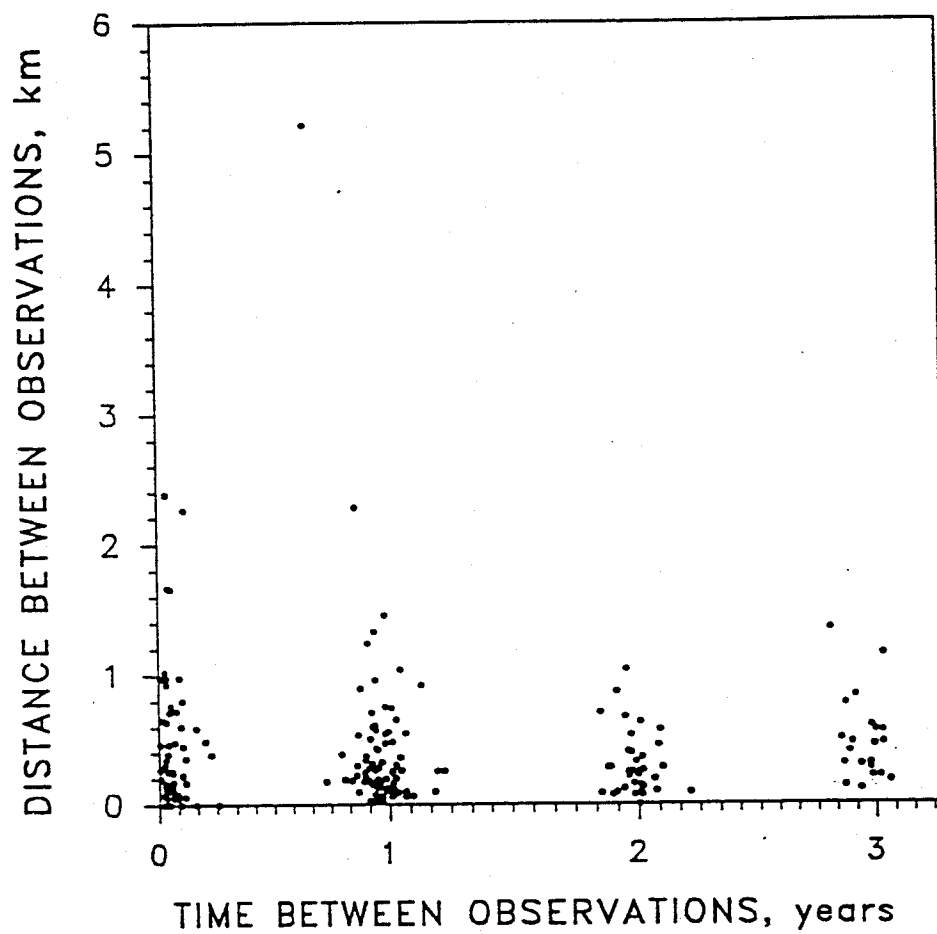


Figure 13 Relationship between distance moved and time between 203 pairs of capture and recapture records of immature hawksbills

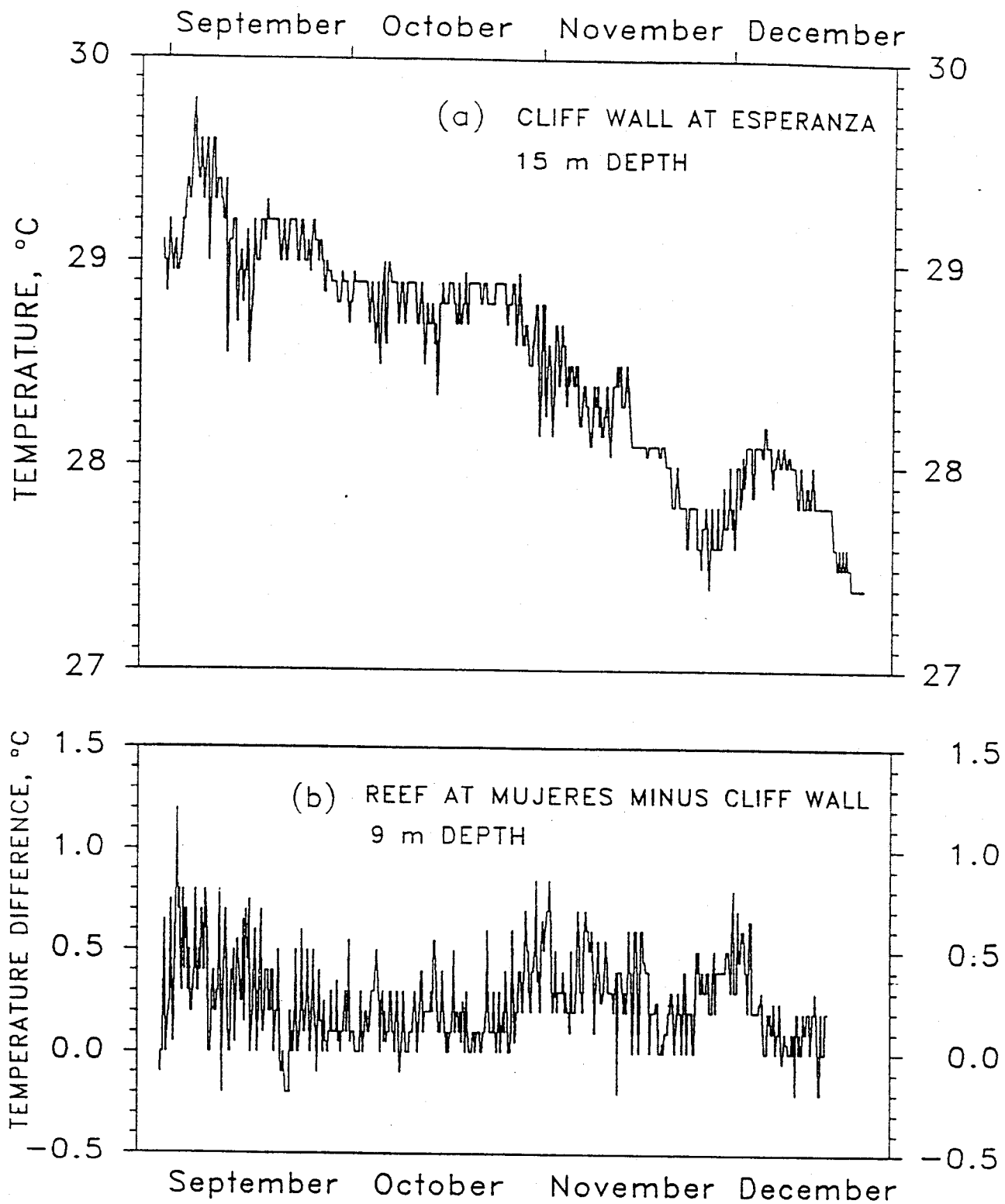


**Figure 14** (a) Ambient water temperature at El Norte  
 (b) Difference in water temperature between the reef at Mujeres  
 and the cliff wall at El Norte (Esperanza cave)

### Seawater temperatures

Water temperatures were monitored at two sites from early September to late December 1995. Hobo-temp temperature dataloggers (model HCI, Onset Computer Corp, Pocasset MA 02559) were waterproofed and programmed to record temperature every 2.7 hours. The dataloggers were calibrated against a high quality mercury thermometer shortly before use. One datalogger was deployed at 15 m depth along the El Norte cliff wall at Esperanza cave, the second datalogger was installed at 9 m depth on the reef at Mujeres. Figures 14a,b illustrate the temperature data obtained. Water temperatures at both sites dropped almost 2°C during the time period examined. Reef site water temperatures were on average 0.25°C higher than at the cliff wall.

### Additional observations

- During our frequent surveys of the Mujeres-Carabinero area, many green turtles were observed but often we were not able to capture these turtles. The escape strategy of the green turtles here is to swim away very rapidly and then hide behind or under any available cover. This as opposed to the hawksbills which are more stationary and seem to rely more on camouflage to avoid predators. Estimated straight carapace length of the green turtles in this area ranges from 25 to 45 cm. These turtles reside in the same habitat as the immature hawksbills and apparently forage on algae. Green turtles were also frequently observed along El Norte and at Monito. They were frequently seen at the surface about 50 meters from the cliff face apparently feeding on floating debris. On one such occasion, a green turtle was observed actively pursuing and eating small reddish-brown colored jellyfish.
- Along El Norte, a number of hawksbills carapace damage suggesting repeated collision with the cliff face. The posterior carapace in these turtles lacked or had very loose post-marginal scutes. Turtles residing in the cliff face areas undoubtedly take precautions to avoid being carried by the often substantial swells into the limestone cliffs. However, the cliff-face frequently has a hazardous overhang about one meter above sea-level (see figure 8a) and turtles probably collide involuntarily with the wall at least once in a while. Hawksbill along El Norte also often have their carapaces covered to varying degrees with white and pink calcareous algae, as opposed to the reef hawksbills of Carabinero-Mujeres and Sardinera which almost always carry red and brown algae.
- No turtles were observed with fibropapillomas.
- One pair of turtles was observed in a plastron to plastron mating position off Carmelitas. Hawksbill mating was also seen at the foot of the booby colony at the eastern part of El Norte. Courtship was observed at El Norte. Two males were seen in mating position (one mounted atop the other) at Esperanza.
- Twenty-seven hawksbill carapacial scute samples were collected for a collaborative age determination study with Dr Ohtaishi (Hokkaido University).
- A total of 83 hawksbill nests and 105 false crawls were counted by us during the first study period from July 17 to August 29, 1995. In the period from December 15 to January 2, 1996 25 nests and 20 false crawls were found.
- Nest temperatures were recorded for 7 nests laid in the second half of August using Hobo-temp dataloggers. These recorders were retrieved and deployed again in late December in six freshly laid nests.



# APPENDIX I

| Date                                         | New/<br>Recap | ID number | Flipper tags  | PIT tag    | Mass<br>[kg] | SCL<br>[cm] |
|----------------------------------------------|---------------|-----------|---------------|------------|--------------|-------------|
| Green turtles ( <u>Chelonia mydas</u> )      |               |           |               |            |              |             |
| 13-Jul-95                                    | N             | 95-008    | SSL230/BP4452 |            | MD           | 30.7        |
| 23-Jul-95                                    | N             | 95-047    | SSL252/BP4456 |            | 5.9          | 36.4        |
| 25-Jul-95                                    | N             | 95-052    | SSL256/BP4456 |            | 3.2          | 30.3        |
| 28-Jul-95                                    | N             | 95-061    | SSL264/SSL265 |            | 2.4          | 27.3        |
| 31-Jul-95                                    | N             | 95-070    | BP4463/SSL268 |            | 6.2          | 35.7        |
| 03-Aug-95                                    | N             | 95-075    | BP4467/SSL270 |            | 27.0         | 59.6        |
| 04-Aug-95                                    | N             | 95-078    | SSL272/BP4469 |            | 3.6          | 30.3        |
| 09-Aug-95                                    | N             | 95-095    | SSM908/BP4475 |            | 3.2          | 30.2        |
| 14-Aug-95                                    | N             | 95-108    | BP4483/SSM918 |            | 5.1          | 33.9        |
| 14-Aug-95                                    | N             | 95-109    | BP4484/SSM920 |            | 5.2          | 34.9        |
| 27-Aug-95                                    | N             | 95-114    | SSM924/SSM923 |            | 2.8          | 28.4        |
| Hawksbills ( <u>Eretmochelys imbricata</u> ) |               |           |               |            |              |             |
| 12-Jul-95                                    | R             | 94-019    | X4624/X4623   | 7F7A002A55 | 2.2          | 26.9        |
| 12-Jul-95                                    | R             | 92-045    | 1414/1415     | 7F7D32183C | 8.5          | 40.7        |
| 12-Jul-95                                    | R             | 93-016    | 1816/BP474    | 7F7D3E214E | 10.6         | 45.0        |
| 13-Jul-95                                    | N             | 95-004    | SSL227/SSL228 | 2242246546 | 1.4          | 23.4        |
| 13-Jul-95                                    | N             | 95-005    | SSL229/BP4451 | 2242291872 | 6.4          | 38.6        |
| 13-Jul-95                                    | R             | 94-075    | SSJ945/SSJ946 | 1F48566B56 | 3.2          | 29.8        |
| 13-Jul-95                                    | R             | 94-094    | SSJ972/SSJ973 | 1F482C115A | 2.2          | 27.9        |
| 13-Jul-95                                    | R             | 94-110    | SSJ995/SSJ994 | 1F5004404D | 2.5          | 27.8        |
| 14-Jul-95                                    | R             | 94-012    | SSL209/X4613  | 7F7D4D104A | 5.2          | 34.4        |
| 14-Jul-95                                    | R             | 94-011    | X4611/X4610   | 22421A057B | 5.6          | 37.1        |
| 14-Jul-95                                    | N             | 95-012    | SSL232/SSL231 | 22422C0937 | 2.8          | 28.9        |
| 21-Dec-95                                    | R             | 95-012    | SSL232/SSL231 | 22422C0937 | 3.1          | 31.1        |
| 14-Jul-95                                    | N             | 95-013    | SSL233/SSL234 | 2242185F69 | 2.8          | 25.3        |
| 14-Jul-95                                    | R             | 94-070    | SSJ939/BP4411 | 1F4A312541 | 8.2          | 38.5        |
| 14-Jul-95                                    | N             | 95-015    | SSL235/SSL236 | 2242373F2C | 1.9          | 25.0        |
| 14-Jul-95                                    | R             | 94-010    | X4609/X4608   | 7F7D4F3756 | 4.0          | 32.0        |
| 14-Jul-95                                    | R             | 92-028    | SSJ940/BP4412 |            | 21.0         | 53.9        |
| 15-Jul-95                                    | R             | 94-036    | X4639/BP497   | 7F7D4E5456 | 5.6          | 35.4        |
| 15-Jul-95                                    | N             | 95-019    | SSL237/SSL239 | 2242153223 | 2.1          | 26.1        |
| 15-Jul-95                                    | R             | 94-052    | SSJ911/SSJ916 | 22422B344A | 2.2          | 26.3        |
| 15-Jul-95                                    | R             | 94-037    | X4640/BP498   | 1F482B2549 | 11.4         | 47.4        |
| 15-Jul-95                                    | R             | 94-026    | X4631/X4632   | 7F7D4D2D71 | 1.8          | 24.3        |
| 15-Jul-95                                    | N             | 95-023    | SSL240/SSL241 | 224217277E | 2.6          | 28.1        |
| 15-Jul-95                                    | R             | 94-104    | SSJ986/SSJ985 | 1F4A4D2E1C | 1.8          | 25.6        |
| 15-Jul-95                                    | N             | 95-025    | SSL242/SSL243 | 22422C4B7A | 1.9          | 25.8        |
| 15-Jul-95                                    | R             | 94-028    |               | 7F7D4D0332 | 1.5          | 23.1        |
| 26-Dec-95                                    | R             | 94-028    |               | 7F7D4D0332 | 1.8          | 25.1        |
| 15-Jul-95                                    | N             | 95-027    |               | 2242230B2B | 1.2          | 21.0        |
| 16-Jul-95                                    | R             | 94-132    | SSL225/SSL224 | 2242190112 | 2.4          | 26.2        |
| 16-Jul-95                                    | R             | 94-102    | SSJ983/SSJ982 | 1F4A222C49 | 2.0          | 25.8        |
| 16-Jul-95                                    | R             | 93-053    | 1524/1525     | 7F7D4D1520 | 4.9          | 34.6        |
| 17-Jul-95                                    | R             | 93-048    | 1509/BP489    | 7F7D4D114B | 15.4         | 49.6        |
| 18-Jul-95                                    | R             | 93-023    | SSJ977/BP476  | 7F7D41504A | 18.5         | 50.8        |
| 18-Jul-95                                    | N             | 95-033    |               | 22421C6A21 | 1.4          | 22.4        |
| 19-Jul-95                                    | N             | 95-034    | SSL244/SSL245 | 22423F2743 | 1.5          | 23.7        |
| 19-Jul-95                                    | R             | 92-030    | 1378/1377     | 7F7D43492B | 3.9          | 31.7        |
| 19-Jul-95                                    | R             | 94-048    | SSJ907/SSJ908 | 2242340C35 | 1.8          | 24.5        |
| 19-Jul-95                                    | R             | 94-084    | SSJ957/BP4419 | 1F4A14394A | 10.8         | 44.0        |

| Date                                                   | New/<br>Recap | ID number | Flipper tags     | PIT tag    | Mass<br>[kg] | SCL<br>[cm] |
|--------------------------------------------------------|---------------|-----------|------------------|------------|--------------|-------------|
| Hawksbills ( <u>Eretmochelys imbricata</u> ) continued |               |           |                  |            |              |             |
| 20-Jul-95                                              | R             | 94-058    | SSJ922/SSJ923    | 1F4A3E6C6D | 3.4          | 30.1        |
| 20-Jul-95                                              | R             | 92-006    | 1185/1186        | 7F7D376426 | 4.7          | 34.0        |
| 21-Jul-95                                              | N             | 95-040    | SSL246/SSL247    | 22421E3875 | 1.9          | 25.7        |
| 21-Jul-95                                              | N             | 95-041    | 1611/1612-BP4454 |            | 71.0         | 83.8        |
| 21-Jul-95                                              | R             | 92-022    | 1361/BP4453      | 22421B186E | 11.4         | 45.7        |
| 22-Jul-95                                              | N             | 95-043    | SSL248/SSL249    | 22423B195A | 2.6          | 28.4        |
| 15-Dec-95                                              | R             | 95-043    | SSL248/SSL249    | 22423B195A |              | 28.4        |
| 22-Jul-95                                              | N             | 95-044    | SSL250           |            | 1.8          | 25.5        |
| 22-Jul-95                                              | R             | 93-020    | 1821/1822        | 7F7D43075C | 3.0          | 29.8        |
| 22-Jul-95                                              | N             | 95-046    | SSL251/BP4455    |            | 60.0         | 78.5        |
| 23-Jul-95                                              | R             | 93-017    | X4605/1818       | 7F7D43005C | 4.3          | 32.6        |
| 23-Jul-95                                              | N             | 95-049    | SSL253/BP4457    |            | 59.0         | 78.3        |
| 23-Jul-95                                              | R             | 94-054    | SSJ913/BP4458    | 1F4A3D302A | 4.4          | 32.4        |
| 24-Jul-95                                              | N             | 95-051    | SSL254/SSL255    | 2242194D37 | 2.0          | 25.3        |
| 25-Jul-95                                              | R             | 92-038    | 1394/1395        | 22421D6047 | 7.8          | 40.0        |
| 25-Jul-95                                              | N             | 95-054    | BP4460/SSL257    | 2242270A04 | 22.0         | 58.1        |
| 25-Jul-95                                              | R             | 94-017    | X4621/X4620      | 7F7D50223B | 4.2          | 33.1        |
| 26-Jul-95                                              | N             | 95-056    | SSL258/SSL259    | 2242351966 | 1.6          | 24.2        |
| 27-Jul-95                                              | R             | 92-016    | 1376/1375        | 7F7D371D27 | 15.4         | 50.3        |
| 27-Jul-95                                              | R             | 94-081    | SSJ953/SSJ952    | 1F4A113B4B | 2.9          | 29.2        |
| 27-Jul-95                                              | N             | 95-059    | SSL261/SSL260    | 2242136C27 | 2.0          | 25.4        |
| 27-Jul-95                                              | N             | 95-060    | SSL262/SSL263    | 224229142E | 2.5          | 28.0        |
| 29-Jul-95                                              | R             | 94-124    | SSL215/BP4447    | 22423D2D56 | 10.3         | 43.3        |
| 29-Jul-95                                              | R             | 94-076    | SSJ947/BP4416    | 2242306A6D | 16.1         | 49.0        |
| 29-Jul-95                                              | R             | 94-095    | BP4425/SSJ974    | 1F482F6802 | 9.0          | 41.7        |
| 29-Jul-95                                              | R             | 94-101    | BP4430/SSJ981    | 7F7D4F744F | 6.0          | 37.0        |
| 30-Jul-95                                              | R             | 94-067    | SSJ932/SSJ934    | 1F484A1639 | 4.4          | 33.0        |
| 30-Jul-95                                              | N             | 95-067    | SSL267/BP4462    |            | >72          | 89.3        |
| 30-Jul-95                                              | N             | 95-068    | SSL266/BP4461    | 2242340A1B | 28.0         | 60.9        |
| 31-Jul-95                                              | R             | 93-022    | 1827/1826        | 7F7E6C137F | 7.0          | 38.8        |
| 31-Jul-95                                              | N             | 95-071    | BP4464/SSL269    | 2242264A69 | 26.0         | 61.4        |
| 01-Aug-95                                              | R             | 93-003    | BP4465/1803      | 7F7D3F5E44 | 5.2          | 35.6        |
| 01-Aug-95                                              | N             | 95-073    | 177/BP4466       |            | 66.0         | 80.3        |
| 02-Aug-95                                              | R             | 93-013    | 1812/BP472       | 7F7D364E7D | 17.4         | 52.1        |
| 01-Jan-96                                              | R             | 93-013    | 1812/BP472       | 7F7D364E7D | 18.0         | 52.4        |
| 03-Aug-95                                              | R             | 93-009    | 1809/BP471       | 7F7D394E61 | 9.2          | 41.4        |
| 03-Aug-95                                              | N             | 95-077    | BP4468/SSL271    |            | 52.0         | 76.8        |
| 04-Aug-95                                              | R             | 94-130    | SSL221/SSL222    | 2242180863 | 3.8          | 31.9        |
| 04-Aug-95                                              | R             | 92-005    | 1183/BP4470      | 7F7D322A18 | 11.2         | 44.8        |
| 05-Aug-95                                              | N             | 95-081    | SSL275/SSL274    | 22422E416F | 2.4          | 28.5        |
| 05-Aug-95                                              | R             | 93-010    | 1811/1810        | 7F7E6B4F24 | 5.9          | 36.7        |
| 05-Aug-95                                              | R             | 93-008    | 1807/1808        | 7F7D364172 | 4.0          | 32.1        |
| 06-Aug-95                                              | N             | 95-084    | SSM901/BP4471    |            | 64.0         | 80.9        |
| 08-Aug-95                                              | N             | 95-085    | BP4474/SSM903    |            | >72          | 87.7        |
| 08-Aug-95                                              | N             | 95-086    | BP4473/SSM902    |            | 71.0         | 83.0        |
| 08-Aug-95                                              | R             | 92-002    | SSJ993/BP4433    | 7F7D41523B | 19.4         | 51.0        |
| 08-Aug-95                                              | R             | 94-069    | SSJ937/BP4472    | 1F4A357270 | 6.9          | 37.8        |
| 08-Aug-95                                              | R             | 94-084    | SSJ968/SSJ967    | 1F4A474709 | 5.2          | 35.0        |
| 08-Aug-95                                              | R             | 94-108    | SSJ992/SSJ991    | 1F47743C6A | 8.3          | 40.4        |
| 08-Aug-95                                              | R             | 94-013    | X4614/X4615      | 7F7D4F2367 | 5.2          | 34.8        |
| 21-Dec-95                                              | R             | 94-013    | X4614/X4615      | 7F7D4F2367 | 5.6          | 37.6        |
| 08-Aug-95                                              | R             | 94-119    | BP4443/SSL208    | 22422C0266 | 17.8         | 51.4        |
| 09-Aug-95                                              | N             | 95-093    | SSM905/SSM904    | 2242330F5D | 2.0          | 25.4        |

| Date | New/<br>Recap | ID number | Flipper tags | PIT tag | Mass<br>[kg] | SCL<br>[cm] |
|------|---------------|-----------|--------------|---------|--------------|-------------|
|------|---------------|-----------|--------------|---------|--------------|-------------|

Hawksbills (Eretmochelys imbricata) continued

|           |   |        |                 |            |      |      |
|-----------|---|--------|-----------------|------------|------|------|
| 09-Aug-95 | N | 95-094 | SSM906/SSM907   | 2242286A56 | 2.0  | 25.9 |
| 09-Aug-95 | R | 92-050 | 1407-BP496/1406 | 22422D1A4A | 20.5 | 54.3 |
| 09-Aug-95 | R | 92-010 | 1192/1193       | 7F7D394C27 | 10.6 | 43.1 |
| 10-Aug-95 | N | 95-098 | BP4477/SSM911   |            | 46.0 | 72.4 |
| 10-Aug-95 | N | 95-099 | SSM910/BP4476   |            | 75.0 | 84.5 |
| 10-Aug-95 | R | 93-024 | SSM913/BP477    | 2242302820 | 33.0 | 62.4 |
| 11-Aug-95 | N | 95-101 | SSM914/BP4478   |            | 43.0 | 74.6 |
| 11-Aug-95 | N | 95-102 | BP4479/SSM912   | 22421F451A | 14.6 | 48.0 |
| 12-Aug-95 | R | 92-046 | BP4480/1417     | 2242131465 | 13.6 | 49.4 |
| 12-Aug-95 | R | 92-009 | 1191/1190       |            | 6.0  | 36.6 |
| 13-Aug-95 | N | 95-105 | SSM915/BP4481   | 2242383E27 | 3.8  | 30.6 |
| 13-Aug-95 | R | 94-003 | SSM916/X4604    | 7F7D4B0F40 | 3.4  | 30.9 |
| 14-Aug-95 | N | 95-107 | BP4482/SSM917   |            | 63.0 | 82.2 |
| 23-Aug-95 | R | 94-128 | SSL220/SSL219   | 2242157828 | 3.6  | 31.0 |
| 23-Aug-95 | N | 95-111 | BP4485/SSM919   |            | 62.0 | 77.8 |
| 25-Aug-95 | N | 95-112 | BP4486/SSM921   | 22421C2B55 | 21.0 | 56.1 |
| 25-Aug-95 | N | 95-113 | SSM922/BP4487   |            | 79.0 | 85.9 |
| 27-Aug-95 | N | 95-115 | SSM926/SSM925   | 22422F3E34 | 1.8  | 25.5 |
| 15-Dec-95 | R | 94-031 | X4638/X4637     | 1F47741412 | 10.3 | 43.5 |
| 15-Dec-95 | N | 95-117 | SSM927/SSM928   | 403553026F | 2.6  | 27.6 |
| 15-Dec-95 | R | 94-064 | SSJ928/SSJ929   | 1F476A2010 | 5.4  | 35.7 |
| 16-Dec-95 | R | 92-025 | SSM929/BP4488   | 7F7D39506C | 11.6 | 47.5 |
| 17-Dec-95 | R | 94-030 | X4635/SSM930    | 4037080312 | 3.4  | 30.9 |
| 20-Dec-95 | R | 94-066 | SSJ933/SSJ931   | 1F484B1539 | 2.3  | 28.1 |
| 21-Dec-95 | N | 95-122 | SSM931/BP4489   | 4037353929 | 22.0 | 55.3 |
| 26-Dec-95 | R | 94-079 | SSJ951/BP4418   | 1F4778257D | 8.2  | 40.8 |
| 27-Dec-95 | N | 95-124 | SSM932/SSM933   | 4039467918 | 1.8  | 24.9 |
| 30-Dec-95 | N | 95-125 | SSM935/BP4490   |            | 65.0 | 79.3 |
| 01-Jan-96 | N | 95-126 | SSM937/SSM936   | 40397F3F77 | 1.6  | 24.5 |
| 03-Jan-96 | N | 95-127 |                 | 4037306F18 | 1.4  | 22.3 |

Nesting hawksbills (Eretmochelys imbricata)

|           |   |               |
|-----------|---|---------------|
| 25-Aug-95 | N | SSM951/SSM952 |
| 17-Dec-95 | N | SSM953/SSM954 |
| 18-Dec-95 | N | SSM955/SSM956 |



APPENDIX II Results of radio-immunoglobulin testosterone assays of serum from 57 juvenile and sub-adult hawksbills caught at Mona Island (1995).

| I.D.   | Testosterone<br>(pg/ml) | Predicted<br>sex | I.D.   | Testosterone<br>(pg/ml) | Predicted<br>sex |
|--------|-------------------------|------------------|--------|-------------------------|------------------|
| 92-046 | 141.00                  | M                | 92-002 | 6.60                    | F                |
| 92-009 | 8.16                    | F                | 94-054 | 127.00                  | M                |
| 95-105 | 110.00                  | M                | 94-069 | 73.70                   | M                |
| 94-003 | 18.20                   | U                | 94-070 | 5.72                    | F                |
| 93-009 | 5.53                    | F                | 94-076 | 91.50                   | M                |
| 93-013 | 3.12                    | F                | 94-094 | 6.98                    | F                |
| 93-010 | 84.80                   | M                | 94-091 | 151.00                  | M                |
| 92-016 | 14.30                   | F                | 94-084 | 153.00                  | M                |
| 92-038 | 97.50                   | M                | 93-023 | 5.14                    | F                |
| 93-008 | 6.23                    | F                | 94-075 | 89.90                   | M                |
| 92-005 | 144.00                  | M                | 95-094 | 6.23                    | F                |
| 93-022 | 6.01                    | F                | 95-081 | 7.18                    | F                |
| 94-010 | 14.30                   | F                | 95-043 | 21.20                   | M                |
| 94-036 | 7.80                    | F                | 95-044 | 25.50                   | M                |
| 94-031 | 11.60                   | F                | 95-005 | 11.60                   | F                |
| 94-012 | 9.75                    | F                | 95-060 | 11.50                   | F                |
| 94-011 | 95.70                   | M                | 95-040 | 68.70                   | M                |
| 94-013 | 78.50                   | M                | 94-072 | 17.70                   | U                |
| 94-017 | 12.10                   | F                | 95-004 | 127.00                  | M                |
| 94-112 | 8.52                    | F                | 95-059 | 10.60                   | F                |
| 95-051 | 2.34                    | F                | 95-034 | 107.00                  | M                |
| 95-023 | 7.38                    | F                | 95-012 | 121.00                  | M                |
| 94-101 | 4.98                    | F                | 95-004 | 5.82                    | F                |
| 93-003 | 92.10                   | M                | 92-050 | 9.75                    | F                |
| 94-095 | 119.00                  | M                | 93-024 | 9.75                    | F                |
| 94-108 | 5.60                    | F                | 95-054 | 4.68                    | F                |
| 94-110 | 60.30                   | M                | 95-068 | 11.50                   | F                |
| 94-067 | 17.00                   | U                | 95-071 | 39.60                   | M                |
|        |                         |                  | 94-154 | 100.00                  | M                |

Note: For immature hawksbill turtles, the testosterone levels  $\leq 16.1$  pg/ml are indicative of females, while levels  $\geq 30$  pg/ml are predicted as males. Turtles falling in the range of 16.1 to 30 pg/ml are labeled as undetermined (U) until further analysis.



## APPENDIX III

### MANUSCRIPT SUBMITTED TO CORAL REEFS

Title: DIVING BEHAVIOR OF IMMATURE HAWKSBILLS (Eretmochelys imbricata) ON THE REEFS OF MONA ISLAND, PUERTO RICO

#### Abstract

Time-depth recorders were attached to immature hawksbill turtles residing on the southwestern reefs of Mona Island, Puerto Rico. Data on diving profiles were obtained from five turtles 27.1 to 51.6 cm straight carapace length, revealing strong similarities in behavioral patterns. During daylight hours turtles were active an average of 11.4 hrs per day, spending 3.7% of time at the surface; mean duration of foraging dives increased with turtle size and varied from 18.5 to 25.8 min. At night turtles were mostly inactive surfacing for 1.6% of the time, with individual mean submergence intervals from 35.2 to 46.6 min. The hawksbills maintained a limited home range with a maximum observed extension of 0.84 km. Predator avoidance and escape responses varied with sea floor topography. Turtle activity was inhibited by the storm-induced suspension of sediment.

#### Introduction

The hawksbill (Eretmochelys imbricata) is a circumtropically distributed, medium sized marine turtle frequently found in association with coral reefs (Márquez M 1990). Juvenile turtles with a carapace length of 20 cm and larger are thought to take up residency in hard-bottom neritic habitats after completing the pelagic post-hatchling life phase (Carr et al. 1966). Adaptations for the coral reef environment include thick, abrasion resistant keratinized carapacial scutes, and characteristic beak-like jaws used for snipping food out of crevices (Pritchard and Trebbau 1984). Juvenile to adult hawksbills feed on a variety of benthic invertebrates (den Hartog 1980). Hawksbills in the Caribbean appear to be primarily spongivorous (Meylan 1988). Although the on-land nesting behavior of Eretmochelys has been described in detail (Deraniyagala 1939; Carr et al. 1966), few other than anecdotal accounts are available on the at-sea behavior of the species. One report by Hirth et al. (1992) describes immature hawksbills swimming and resting at a fringing reef in Papua New Guinea.

In this paper, we document the diving behavior observed in immature hawksbills at a reef site in the northern Caribbean. We compare the behavior of this species with that of the more extensively studied green turtle (Chelonia mydas), which has a distribution and habitat preferences comparable to that of the hawksbill.

#### Study Area and Methods

Data were collected during the 1992 to 1994 field seasons (July-November) in a study area along the southwestern coast (18°05'N, 67°57'W) of Mona Island, Puerto Rico (Fig. 1). The study area was divided into three sections named according to the adjacent beaches: Sardinera, Mujeres, Carabinero. Whereas all sections lie on the leeward side of the island and are thus relatively protected from the winds and associated waves that prevail from the east and southeast, substantial differences exist in their structural and biotic properties. The Sardinera section of the study area consists of a forereef with spurs and grooves at between 5 and 12 m water depth, radiating outwards from a fringing/barrier reef.

The reef spur structures seldom reach more than 1.5 m above the substrate. Beyond 12 m depth, about 400 m offshore, the system breaks up into large, sand-separated coral patches. Cover at 10 m depth is dominated by macro-algae, scleractinians, plexaurids and gorgonians. At Mujeres, the reef patches at 4 to 18 m depth are better developed, with typical structure heights of 1 to 2 m (up to 4 m) and overhangs and ledges providing turtles with ample shelter. Patches are covered with an assembly of macro-algae, hydrocorals, scleractinians, plexaurids, gorgonians, and the prominent encrusting sponge Anthosigmella varians. At Carabinero, a hard-bottom terrace is interrupted at 11 m depth, as close as 150 m from shore, by a vertical drop-off exceeding 75 m in depth. The narrow, almost flat terrace has extensive stands of Pseudopteroqorgia sp. upon a substrate covered with Dictyota sp. and other macro-algae. Prominent sponges are Aplysina sp., Tethya sp., and Xestospongia muta.

The repeated observation and capture of numerous tagged immature hawksbills in the nearshore area demonstrated the feasibility of deploying and recovering recording instruments on the turtles. Detailed diving data were then collected by the attachment of custom built time-depth recorders (TDRs) to turtles caught at the study site. Turtles were hand captured during in waters up to 18 m deep by freediving and occasionally with the aid of SCUBA, and brought aboard a small boat for tagging, measurement and TDR application. All turtles used in this experiment were determined to be immature using size criteria. For individual identification turtles had external stainless steel and plastic tags applied to the trailing margin of both front flippers and a Passive Integrated Transponder (PIT) tag inserted subcutaneously to the right front flipper. Size measurements taken of turtles include straight line carapace length (from the anterior nuchal notch to the posteriormost marginal scute) using 40 and 117 x 0.1 cm Haglof aluminum tree calipers, and body mass by weighing with a 20 x 0.1 kg Pesola spring scale. Instrumented turtles were returned to the location of capture within 30 min. Capture locations were determined with a Global Positioning System (GPS) receiver. Throughout most visits to the study area bathymetric information was collected by simultaneously recording depth and location on a portable computer linked to a ultrasonic depth sounder and a GPS receiver.

Two rectangular, epoxy encapsulated electronic TDRs were used, both measuring approximately 2.5 x 3 x 5 cm. TDR-1 weighed 102 g in air, 35 g in water and was later modified with an additional battery making the unit weigh 135 g in air, 47 g in water. TDR-2 weighed 85 g in air and 28 g in water. The digital TDRs were designed to sample and record ambient water pressure at 8 s intervals for a maximum 12.1 d duration. The units were calibrated using a standard pressure station at Scripps Institution of Oceanography. TDR-1 had a water depth resolution of 0.29 m and maximum registerable depth of approximately 110 m. Resolution and maximum reading depth of TDR-2 was 0.36 m and 85 m, respectively. TDRs were attached to the post-marginal scutes of turtles using two round headed #10 stainless steel screws of appropriate length. The screws were fitted with nylon washers to reduce abrasion against the carapace and inserted through holes made with a hand drill along the non-living tissue scute margins. The post-marginal scutes were chosen as the attachment site to minimize the instrument's impact on the turtle and to ensure eventual disattachment by natural outgrowth should we fail to recapture the animal for device recovery.

To facilitate turtle recapture and instrument recovery, a sonic pinger tag was attached to two TDR equipped animals. The cylindrical 10 x 1.8 cm tags (model CHP-87-L, 37 kHz, Sonotronics, Tucson, Arizona, USA) were attached with nylon coated stainless steel wire (crimped with a corrodible copper link) through two 1.5 mm holes in the edge of appropriate posterior marginal carapace scutes. An underwater acoustic locator receiver (model N15A235B, Dukane Corp, St. Charles, Illinois, USA) was used to monitor tagged animals during the TDR deployment period and to facilitate their recapture for instrument recovery.

## Results

Five TDR equipped immature hawksbills released and recaptured in the study area

yielded continuous behavioral records of between 10.0 and 12.1 days duration (Table 1). All turtles exhibited similar behavioral patterns, making an average 48.6 dives per day (standard error 5.1, range 37 to 64). Any submergence beyond a depth of one meter was considered a dive. Two types of dives are recognized: foraging dives featuring continuous depth fluctuations throughout each submergence interval, and resting dives in which little change in measured depth is observed, other than variation attributable to wave action and surfacing descents and ascents. Fig. 2 illustrates this classification for dives made during a 24 hr period by turtle 93-016. Foraging dives coincided with daylight hours (05:45-19:15 hrs on 1 August 1994), and resting dives were made throughout the night. This diel pattern was observed in all turtles and is further summarized in Fig. 3. The hawksbills made foraging dives for an average 11.4 hours per day, surfacing 3.7% of the time during daylight hours and 1.6% at night.

For the comparison of foraging and resting dive characteristics, the dive data was separated according to dive type (Table 2). In each of the turtles, foraging dives were of significantly shorter duration (Fig. 4) than resting dives (one tailed t-tests, assuming independence of samples;  $P < 0.001$ ). Dive depths were positively and significantly correlated with the durations of foraging dives ( $0.3298 \leq r \leq 0.6505$ , Pearson product moment;  $P < 0.001$ ; see Fig. 5) and the subsequent post-dive surface intervals in all turtles ( $0.3156 \leq r \leq 0.6001$ ). Resting dive durations and post-dive surface intervals however were not consistently correlated with dive depths. The depth ranges of foraging and resting dives were similar in all turtles (Fig. 6). Foraging dive durations and post-dive surface intervals were turtle size dependent, increasing significantly with straight carapace length ( $r = 0.4019$  and  $0.4408$ , respectively).

The greatest depth reached by the hawksbills was 24.1 m by turtle no. 94-128 (Fig. 7), shortly after release at Carabinero. At this location the shallow (up to 10 m) hard bottom terrace gives way to an abrupt vertical drop-off. Although the turtle was not pursued immediately after its release, the profiles of the dives made by the animal reflect an escape response observed frequently in other immature hawksbills at the site. Fleeing turtles on the terrace typically swim directly to the dropoff and down, then level off and continue parallel to the wall, appearing again further along the wall at the terrace's edge. The immature hawksbills of the reef patches at Sardinera and Mujeres, with no immediate access to deep water, employed different predator avoidance and escape strategies. We observed these turtles to either remain motionless until approached very closely or to swim away steadily, preferably against the prevailing current. The diving behavior of the TDR equipped patch reef turtles immediately following release reflects both these strategies. In all cases, turtles resumed their diving behavior normal for the time of day within one hour of release.

The response of turtles to inclement weather was observed when a storm front early on 11 September 1994 brought heavy rains and strong waves to Mona Island. The storm caused a temporary deterioration of underwater visibility at the Sardinera site due to stirred up sediment and possibly some terrestrial rain water run-off. The diving record of turtle 94-110 residing in the area revealed that the animal responded by remaining inactive for a large portion of the day during the reduced visibility conditions. The turtle resumed its activity by the late afternoon when the storm had abated and underwater visibility was improved.

Movements of immature hawksbills in the study area were limited. During the TDR deployment period the turtles ventured only several hundred meters away, as evidenced by the proximity of turtle release and recapture locations (Table 1), the limited range of diving depths, and the results of sonic tracking. The sonic tag equipped turtles 94-110 and 94-128 were observed having moved up to 0.31 and 0.84 km from the release site (after 8 and 5 days, respectively), but were substantial closer upon recapture. Further evidence for a limited home range and residency of the immature hawksbills is provided by the close proximity of all reobservations in subsequent years of individuals tagged by us on the reef.

## Discussion and conclusions

The immature hawksbills we studied exhibited diel behavioral patterns similar to those observed by Ogden et al. (1983) for juvenile green turtles on feeding grounds in the US Virgin Islands. Both turtle species were largely active during daylight hours and usually dormant at night. Occasional nightly activity by green turtles was observed by both Bjorndal (1980) and Ogden et al. (1983) on shallow, nearshore grazing plots. The immature hawksbills of the Mona Island study areas did not exhibit such activity, even though on moonlit nights light levels on the reef appear sufficient for visual orientation (pers. observ.). The lack of nightly hawksbill foraging activity may be attributed to the patchy distribution of prey sponges, differing substantially from the homogeneous stands of seagrasses on which green turtles graze. Avoiding detection by large, nocturnally active predators such as sharks may be another incentive for immature reef hawksbills to remain inactive at night. Juvenile hawksbills are frequently found in the stomachs of large tigersharks, Galeocerdo cuvier (Cadenat 1957).

The immature green turtles observed by Ogden et al. (1983) moved between distinct feeding and resting areas differing in depth and biotic composition. We did not observe such commuting of Eretmochelys on the reefs of Mona Island. Depth gradients are present throughout our study area and therefore the similar depth ranges of routine hawksbill foraging and resting dives are indicative of overlapping foraging and resting habitats within the home range. Our results correspond with the repeated sightings of tagged hawksbills at fixed locations as reported by Boulon (1983) and Bjorndal et al. (1985), furthermore supporting the observation by Pritchard and Trebbau (1984) that hawksbills appear to be relatively sedentary after reaching a good feeding area. However, records of migrations by immature Caribbean hawksbills as reported by Boulon (1989) demonstrate that these turtles occasionally venture well beyond their home range.

Inactivity was the response measured in one hawksbill to a reduction in visibility through the suspension of sediment in a usually clear water habitat. The short term, storm-induced event is indicative of the effects on behavior of turtles during the initial phase of habitat sedimentation and emphasizes the reliance of these animals on visual cues for orientation in the reef habitat. Sediment-laden rivers and runoff from coastal development affect many nearshore areas of the island of Puerto Rico (Velazco-Domínguez et al. 1985), where hawksbills have suffered a decline in abundance (D. Corales USFWS, pers. commun.). Persistent sedimentation to the degree of inhibiting the visual orientation of these large animals may prompt turtles to abandon their home range habitat. Occasional long distance migrations observed in the normally sedentary immature hawksbills (Boulon 1989; Moncada G 1994) may be due to the sensitivity of these animals to such habitat deterioration.

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## Figures

Fig. 1. Chart of the nearshore study area along the southwestern coast of Mona Island, Puerto Rico. Isobaths beyond 20 m depth are not plotted. Symbols refer to the release (RL) and recapture (RC) locations of immature hawksbills fitted with time-depth recorders.

Fig. 2. Diving in the 41.8 cm (straight- line carapace length) hawksbill 93-016 during a 24 hr segment starting on 1 August 1994 at 06:00 hrs. Submergences exhibiting continuous variation in measured depth throughout the dive are labeled foraging dives; the remaining dives with little depth variation other than attributable to wave action and surfacing ascents and descents are named resting dives.

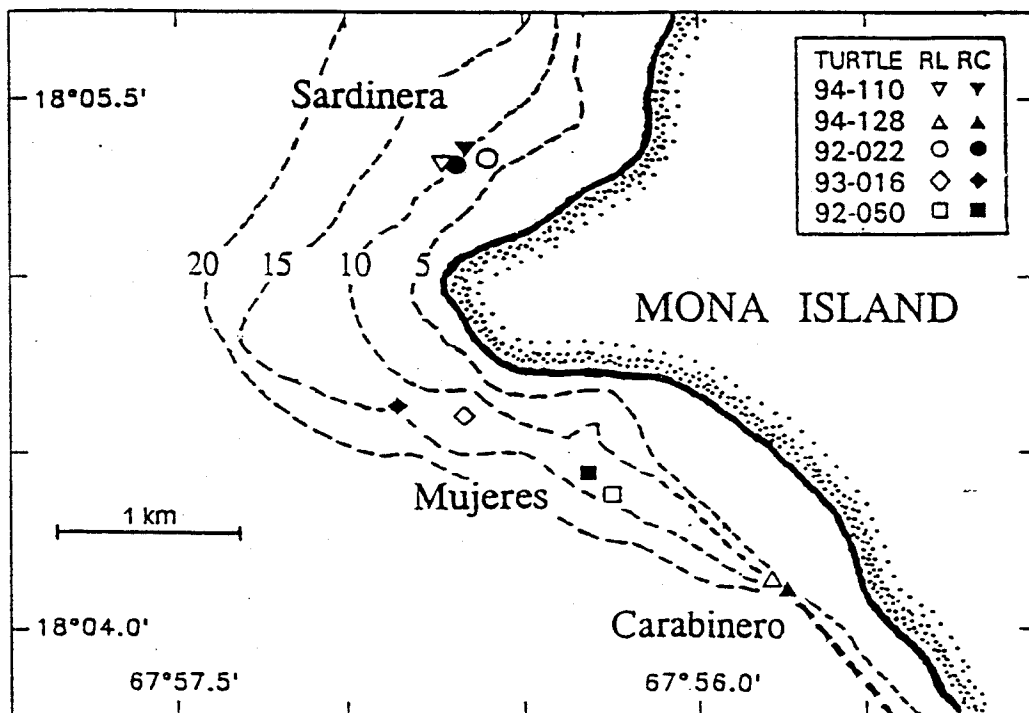
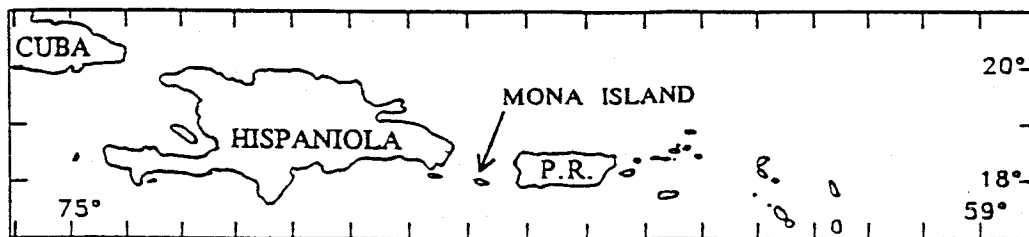
Fig. 3. Diel behavioral pattern as recorded in five immature hawksbills. Percent time turtles spent during surfacings, resting and foraging dives are presented in twenty-four 1-hr segments. The daylight period during the study extended from 05:45-6:40 to 18:00-19:20 hrs local time.

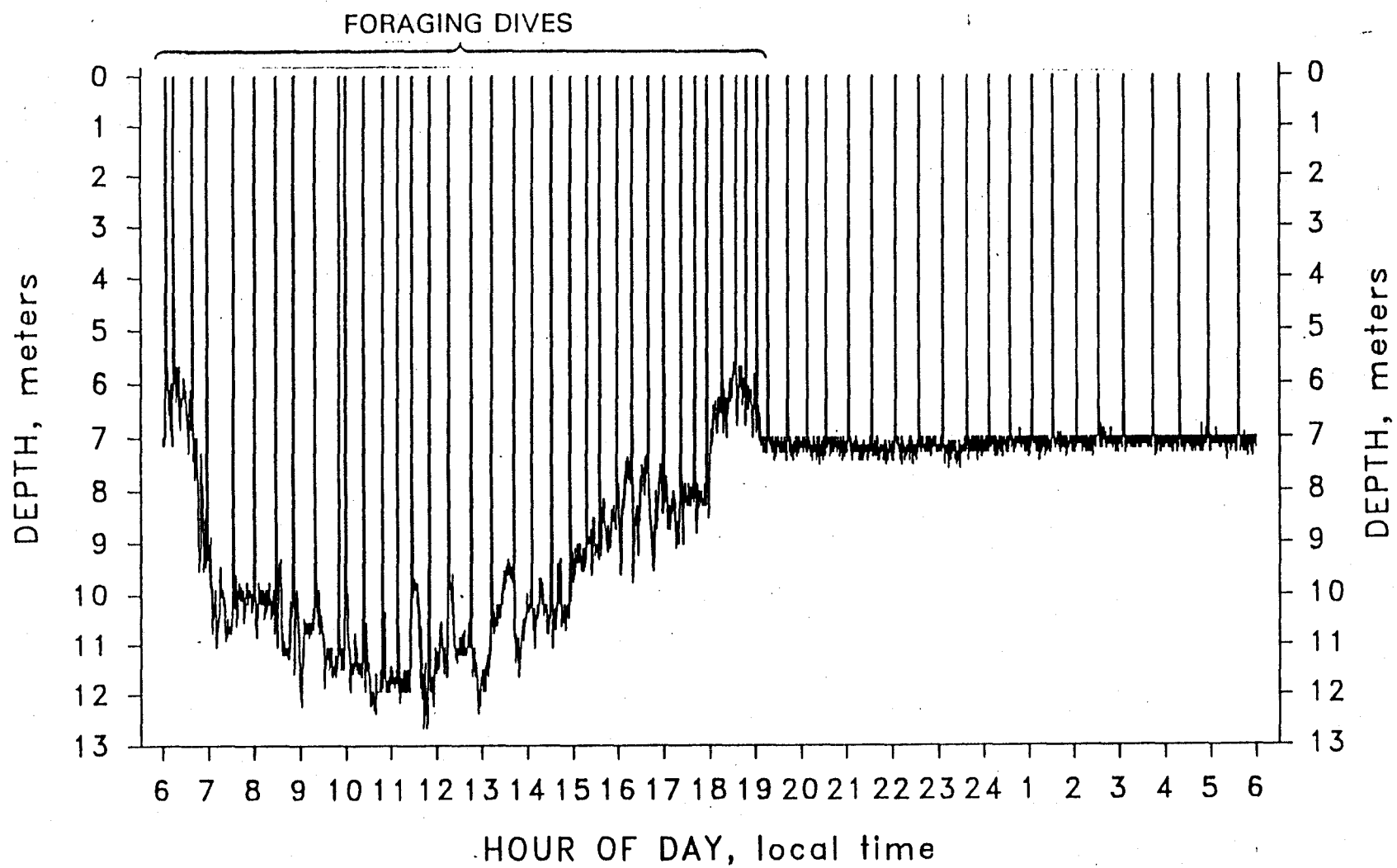
Fig. 4. Dive duration distribution in minutes of 1752 foraging and 987 resting dives as proportion of all dives made by five immature hawksbills.

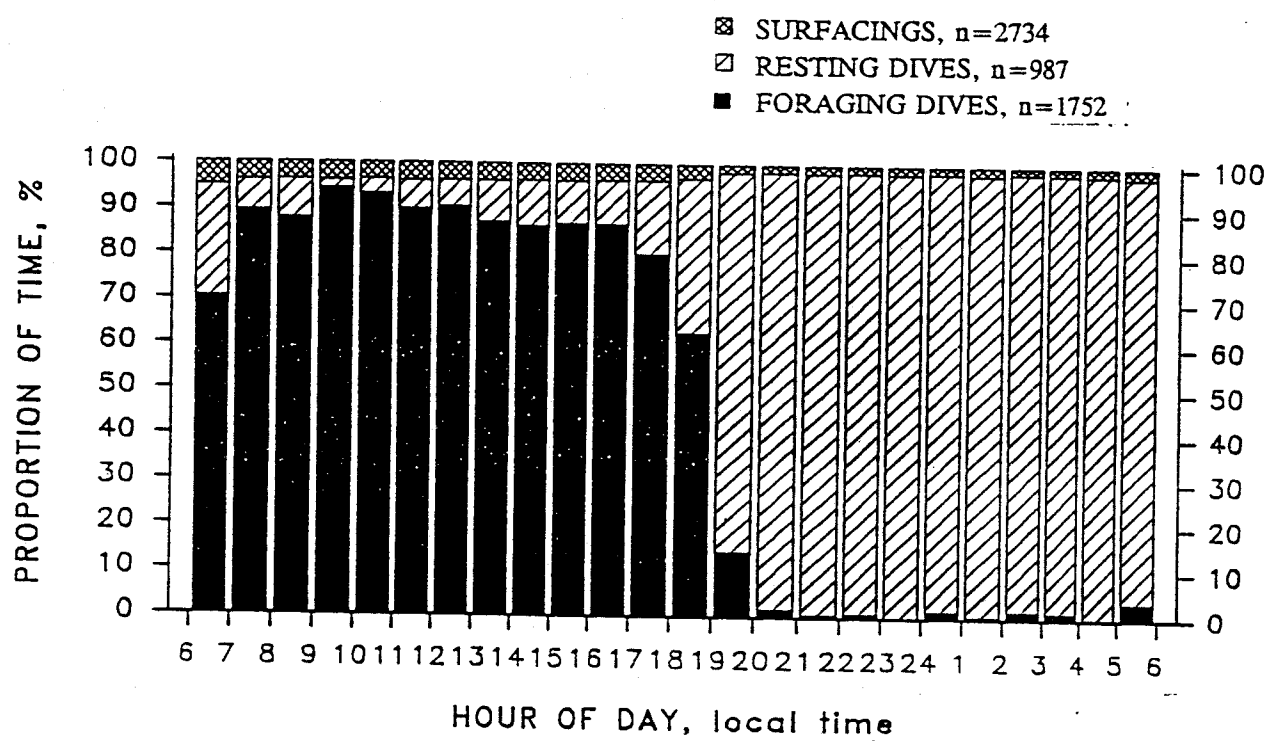
Fig. 5. Distribution by depth of foraging (black) and resting dives (diagonals) as proportion of all dives made by each of five immature hawksbills. Means per dive were calculated as average depth during the submergence interval, including surfacing descents and ascents.

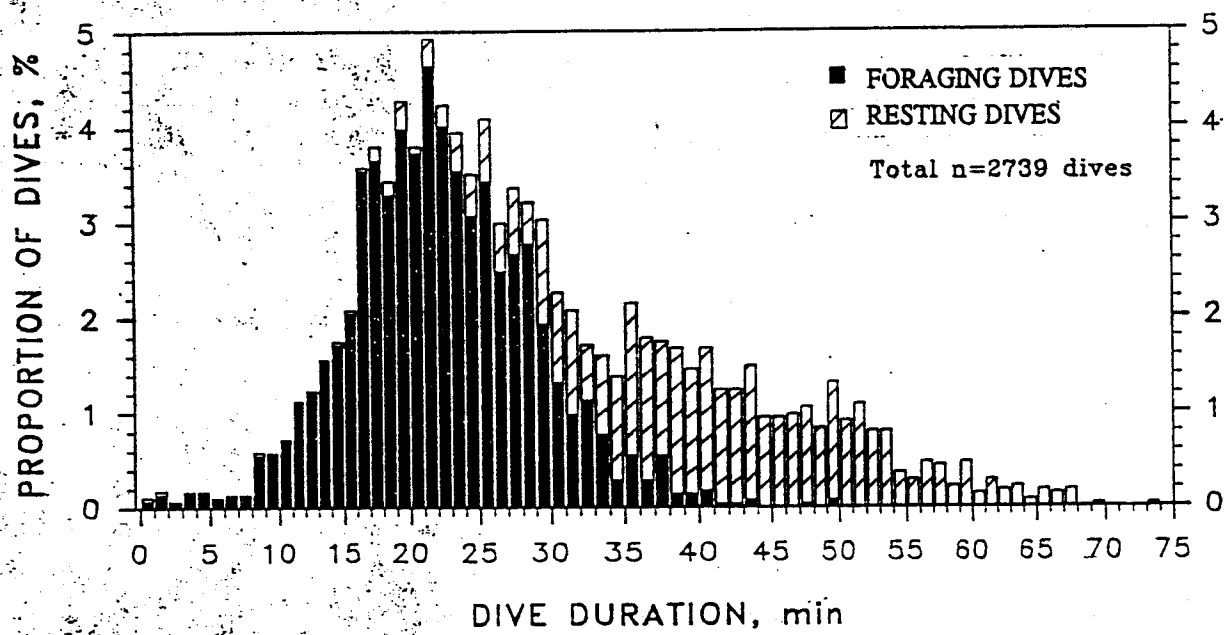
Fig. 6. Dive duration in relation to mean dive depth for 1752 foraging dives made by five immature hawksbills.

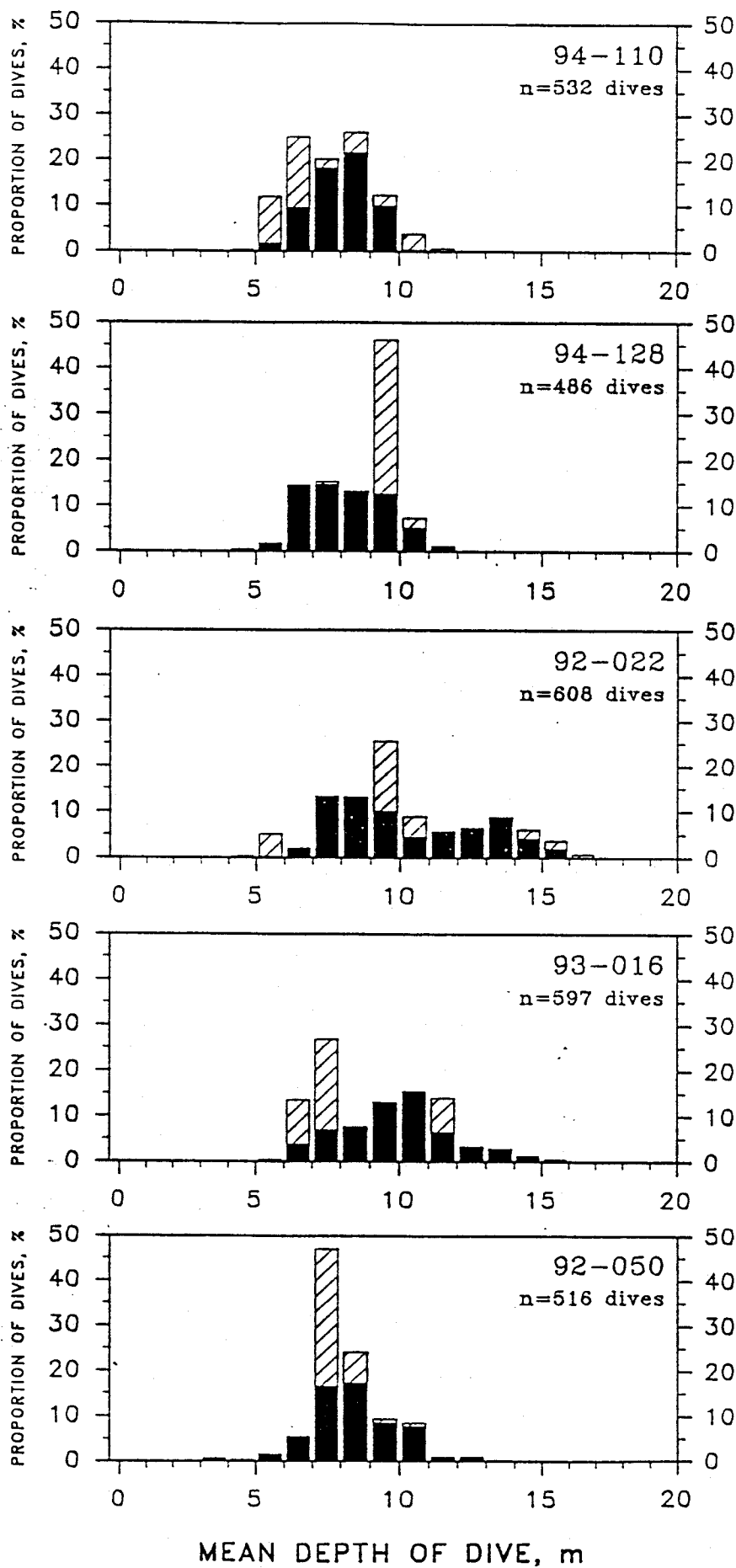
Fig. 7. Diving in the 29.3 cm (straight- line carapace length) hawksbill 94-128 upon release at 11:07 hrs on 5 November 1994. The dives made immediately after release reflect the escape response observed repeatedly in hawksbills at Carabinero.

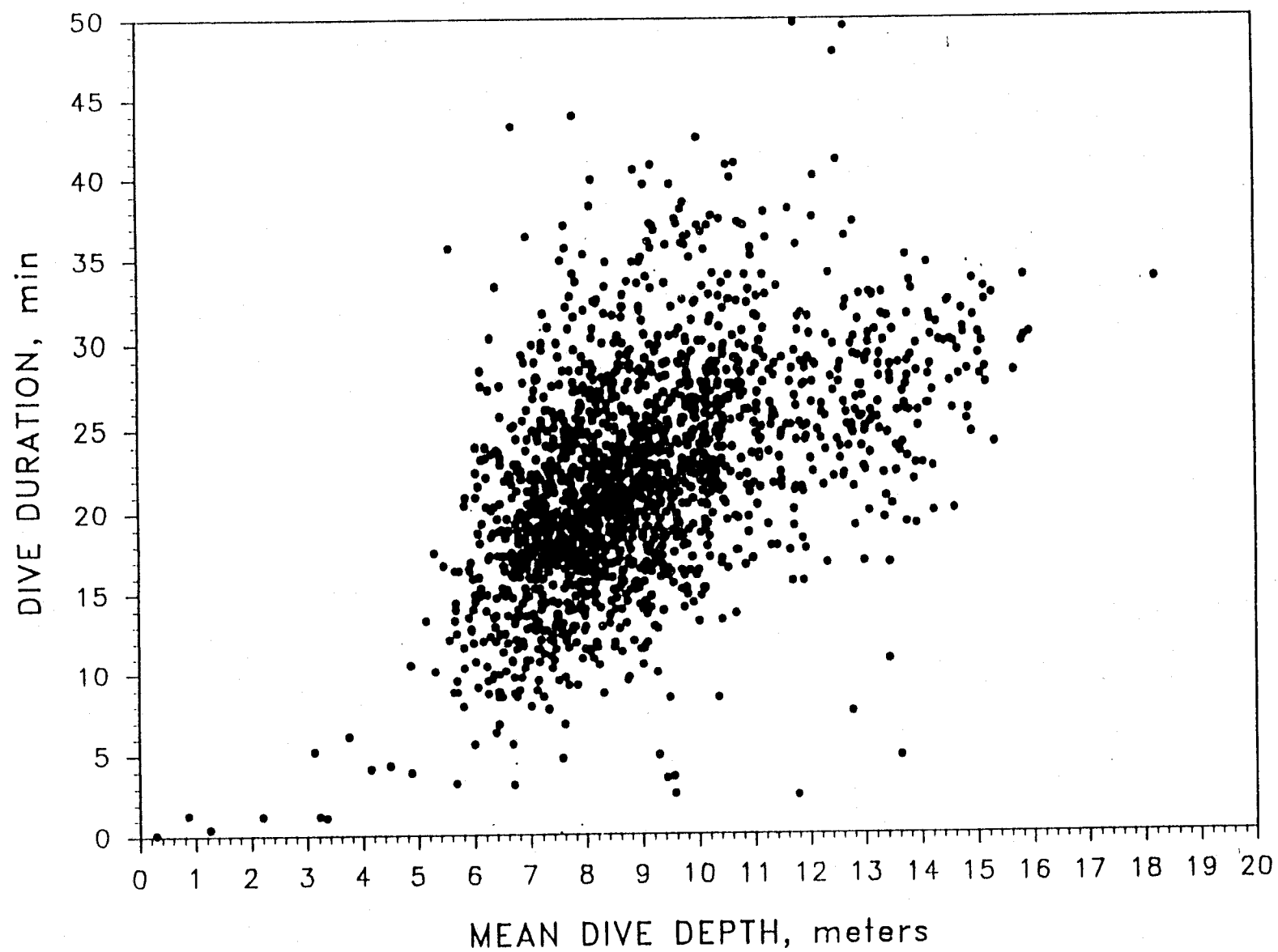












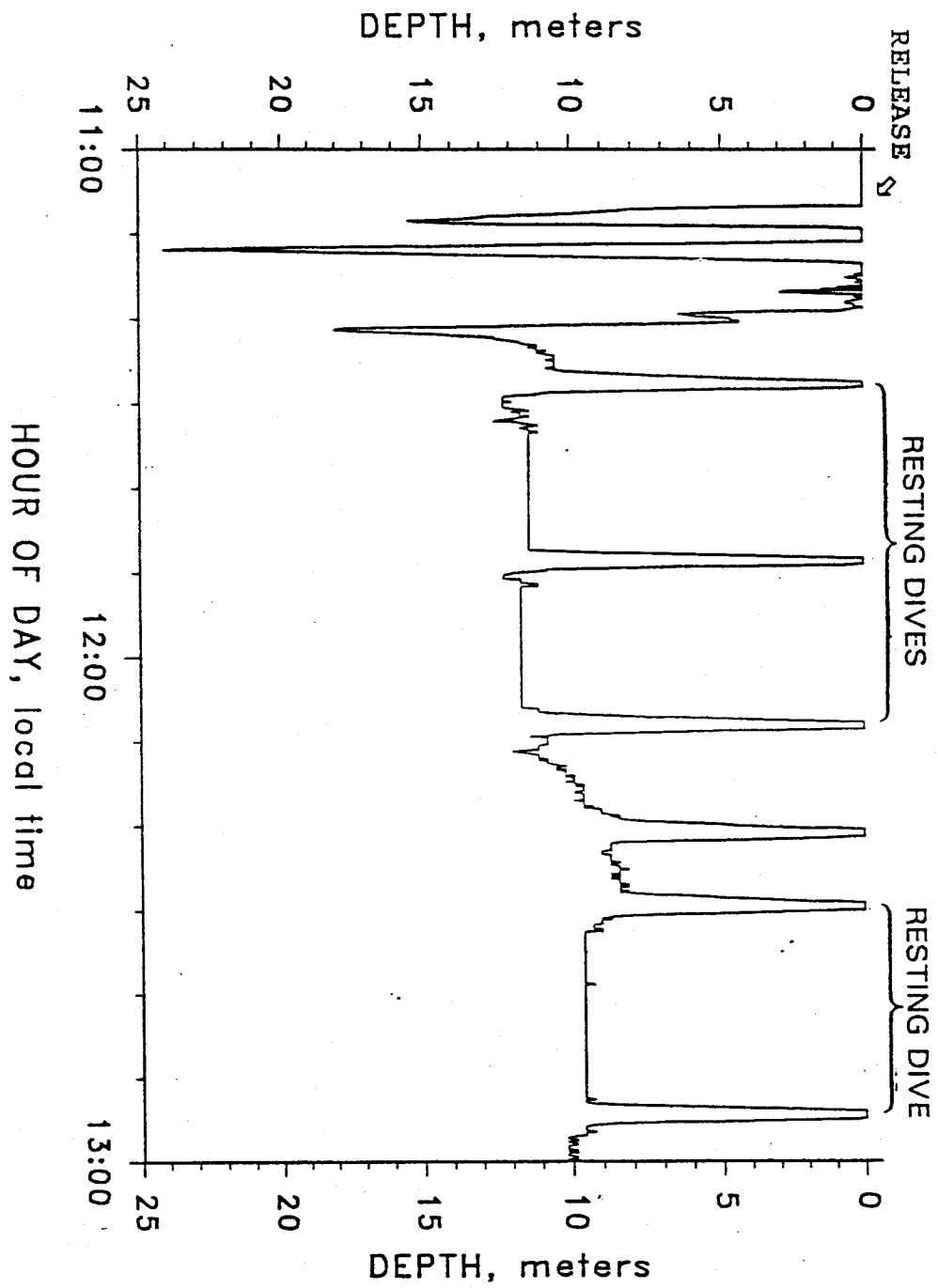


Table 1. Biological and experimental data of five time-depth recorder equipped immature hawksbill sea turtles. Turtle behavior was monitored continuously from the time of instrument deployment. Net distance moved is the distance between turtle capture locations of instrument deployment and recovery. The experiment was conducted along the southwest coast of Mona Island, Puerto Rico.

| Turtle no. | Straight-line<br>carapace<br>length (cm) | Body mass<br>(kg) | Instrument<br>deployed | Date and time<br>of instrument<br>deployment | Date and time<br>of instrument<br>recovery | Length of<br>behavioral<br>record (d) | Net distance<br>moved (km) |
|------------|------------------------------------------|-------------------|------------------------|----------------------------------------------|--------------------------------------------|---------------------------------------|----------------------------|
| 94-110     | 27.1                                     | 2.4               | TDR-1                  | 9 Sep 1994<br>11:07                          | 17 Sep 1994<br>15:55                       | 10.2                                  | 0.14                       |
| 94-128     | 29.3                                     | 3.1               | TDR-1                  | 5 Nov 1994<br>11:07                          | 15 Nov 1994<br>10:36                       | 10.0                                  | 0.10                       |
| 92-022     | 38.5                                     | 7.4               | TDR-1                  | 9 Aug 1993<br>15:13                          | 23 Aug 1993<br>17:45                       | 12.0                                  | 0.25                       |
| 93-016     | 41.8                                     | 8.8               | TDR-1                  | 27 Jul 1994<br>15:55                         | 16 Aug 1994<br>16:36                       | 12.1                                  | 0.34                       |
| 92-050     | 51.6                                     | 18.4              | TDR-2                  | 2 Aug 1994<br>12:15                          | 25 Aug 1994<br>10:41                       | 12.1                                  | 0.17                       |

Table 2. Summary of immature hawksbill diving data after partitioning into foraging and resting dives (for separation criteria, see text).

|                | Turtle<br>no. | n   | Post-dive surface<br>interval (s)<br>mean $\pm$ SE<br>min - max | Dive duration<br>(min)<br>mean $\pm$ SE<br>min - max | Dive depth<br>(m)<br>mean $\pm$ SE | Maximum depth<br>recorded (m) |
|----------------|---------------|-----|-----------------------------------------------------------------|------------------------------------------------------|------------------------------------|-------------------------------|
| FORAGING DIVES | 94-110        | 326 | 36.6 $\pm$ 0.5<br>8 - 64                                        | 18.9 $\pm$ 0.3<br>1.2 - 43.5                         | 7.9 $\pm$ 0.1                      | 11.9                          |
|                | 94-128        | 308 | 48.5 $\pm$ 1.0<br>8 - 200                                       | 18.5 $\pm$ 0.3<br>0.4 - 38.1                         | 8.1 $\pm$ 0.1                      | 24.1                          |
|                | 92-022        | 429 | 59.8 $\pm$ 0.7<br>8 - 120                                       | 22.0 $\pm$ 0.3<br>0.1 - 39.6                         | 10.2 $\pm$ 0.1                     | 17.5                          |
|                | 93-016        | 373 | 51.9 $\pm$ 0.8<br>8 - 112                                       | 24.2 $\pm$ 0.3<br>3.5 - 36.5                         | 9.9 $\pm$ 0.3                      | 21.2                          |
|                | 92-050        | 316 | 64.4 $\pm$ 1.1<br>8 - 152                                       | 25.8 $\pm$ 0.5<br>1.1 - 49.7                         | 8.4 $\pm$ 0.1                      | 17.4                          |
| RESTING DIVES  | 94-111        | 206 | 36.1 $\pm$ 0.7<br>8 - 72                                        | 39.7 $\pm$ 0.6<br>1.7 - 57.2                         | 7.1 $\pm$ 0.1                      | 12.1                          |
|                | 94-128        | 178 | 50.2 $\pm$ 1.1<br>8 - 96                                        | 46.6 $\pm$ 1.0<br>0.7 - 73.7                         | 9.6 $\pm$ 0.0                      | 12.2                          |
|                | 92-022        | 179 | 51.9 $\pm$ 1.1<br>24 - 128                                      | 41.0 $\pm$ 0.7<br>17.6 - 59.3                        | 9.9 $\pm$ 0.2                      | 17.5                          |
|                | 93-016        | 224 | 36.6 $\pm$ 1.5<br>8 - 152                                       | 35.2 $\pm$ 0.5<br>17.6 - 59.3                        | 8.0 $\pm$ 0.1                      | 14.0                          |
|                | 92-050        | 200 | 60.2 $\pm$ 1.8<br>24 - 216                                      | 43.7 $\pm$ 0.8<br>14.7 - 66.3                        | 8.0 $\pm$ 0.0                      | 11.6                          |



## APPENDIX IV

MANUSCRIPT SUBMITTED TO MARINE BIOLOGY

### DIVING BEHAVIOR OF IMMATURE HAWKSBILLS IN A CARIBBEAN CLIFF WALL HABITAT

Running head: HAWKSBILL DIVING BEHAVIOR

#### Abstract

Time-depth recorders were attached to immature hawksbills residing at the northwestern cliffs of Mona Island, Puerto Rico. Data on diving profiles were obtained from four turtles 32.0 to 53.4 cm straight carapace length, revealing strong similarities in behavioral patterns. During daylight hours turtles were active an average 8.4 hrs per day, surfacing 3.6% of the time. Length of foraging dives correlated with turtle size with mean durations ranging from 8.6 to 14.0 min. Foraging dives, with a mean depth of 4.7 m, were associated with feeding on encrusting sponges. At night turtles were mostly inactive surfacing 1.8% of the time and with individual mean submergence intervals of between 30.4 and 37.1 min. From the surfacing behavior of turtles making deep and long dives it is inferred that dives were aerobic and used oxygen stores in tissues other than the lung.

#### Introduction

Juveniles of the circumtropically distributed hawksbill turtle (Eretmochelys imbricata) are thought to take up residence in benthic habitats after the pelagic post-hatchling life phase (Carr, 1966). Information available on the behavioral ecology of juvenile and subadult hawksbills is limited and consists mainly of anecdotal observations of wild and captive turtles, and inferences made from collected specimens. Behavioral studies of the species have largely focused on nesting females when animals are most accessible to researchers.

The hawksbill is well adapted for mechanically harsh benthic environments with the carapace of the species featuring thick, abrasion resistant keratinized scutes. Characteristic beak-like jaws are used for snipping food out of crevices (Carr, 1966). The hawksbill diet consists of a wide variety of benthic invertebrates (den Hartog, 1980) and, particularly in the Caribbean, of sponges (Meylan, 1988).

Due to the highly alert and mobile nature of sea turtles, it is difficult to make behavioral observations of the animals for extended time periods in the marine environment. Indirect methods are frequently used and detailed behavioral information of turtles has been gathered with recording devices attached to the animals. Eckert et al. (1989) demonstrated with time-depth recorders the diel periodicity and deep diving capabilities of leatherback sea turtles (Dermochelys

coriacea) during interesting periods on St. Croix, US Virgin Islands. Similarly, Sato et al. (1994) used recorder technology to examine the thermal characteristics and diving behavior of loggerhead sea turtles (Caretta) between nestings in Japan.

Published information on the behavioral patterns of free ranging immature marine turtles is much less detailed. Standora et al. (1984) monitored the surfacing patterns and movement of one subadult leatherback for a period of 18 h off the coast of Rhode Island, USA. The behavior of juvenile green turtles (Chelonia mydas) on foraging grounds at St. Croix was studied for periods of up to 12 d by Ogden et al. (1983), revealing marked diel foraging patterns. In this paper we report on a detailed study of the diving behavior of immature hawksbill sea turtles inhabiting the vertical cliff walls of Mona Island. We establish the depth range of feeding and resting habitats, and examine the activity patterns of these turtles. Furthermore, we explore the physiological basis for the observed dive types.

#### Materials and methods

Data were obtained from August to November 1994 along the northwestern coast (18°07'N, 67°55'W) of Mona Island, Puerto Rico. The study site (Fig. 1) consists of a 2.3 km section of cliff coast where a gently upward-sloping bedrock seafloor meets the vertical limestone cliff-face at 18 to 34 m depth. The cave-strewn wall of the cliff is heavily populated with an epifaunal assembly consisting of encrusting Porifera, calcareous and phaeophytic algae, and numerous other invertebrates. We found evidence for residency there of a population of hawksbills by repeated observations of physically distinctive and tagged individuals during field work from 1992 through 1994. Detailed diving data were collected by the attachment of custom built time-depth recorders (TDRs) to turtles caught at the study site. Turtles were hand captured during daylight hours by freediving or with the aid of SCUBA and brought aboard a small boat for tagging, measurement and TDR application. All turtles participating in this experiment were immature, determined by applying size criteria. For individual identification turtles had external stainless steel and plastic tags applied to the trailing margin of both front flippers and a Passive Integrated Transponder (PIT) tag inserted subcutaneously to the right front flipper. Size measurements taken of turtles include straight line carapace length (from the anterior nuchal notch to the posteriormost marginal scute) using 40 and 117 x 0.1 cm Haglof aluminum tree calipers, and body mass by weighing with a 20 x 0.1 kg Pesola spring scale. Instrumented turtles were returned to the location of capture within 30 min. Capture locations were determined by using landmarks and a Global Positioning System (GPS) receiver.

Two rectangular, epoxy encapsulated electronic TDRs were used, both measuring approximately 2.5 x 3 x 5 cm. TDR-1 weighed 102 g in air, 35 g in water and was later modified with an additional battery making the unit weigh 135 g in air, 47 g in water. TDR-2 weighed 85 g in air and 28 g in water. The digital TDRs were designed to sample and record ambient water pressure at 8 s intervals for a maximum 12.1 d duration. The units were calibrated using a standard pressure station at Scripps Institution of Oceanography. TDR-1 had a water depth resolution of 0.29 m and maximum registerable depth of approximately 110 m.

Resolution and maximum reading depth of TDR-2 was 0.36 m and 85 m, respectively. TDRs were attached to the post-marginal scutes of turtles using two round headed #10 stainless steel screws of appropriate length. The screws were fitted with nylon washers to reduce abrasion against the carapace and inserted through holes made with a hand drill along the non-living tissue scute margins. The post-marginal scutes were chosen as the attachment site to minimize the instrument's hydrodynamic impact on the turtle and to ensure eventual disattachment by natural outgrowth should we fail to recapture the animal for device recovery.

To facilitate turtle recapture and instrument recovery, a sonic pinger tag was attached to three TDR equipped animals. The cylindrical 10 x 1.8 cm tags (model CHP-87-L, 37 kHz, Sonotronics, Tucson, Arizona, USA) were attached with nylon coated stainless steel wire (crimped with a corrodible copper link) through two 1.5 mm holes in the edge of appropriate posterior marginal carapace scutes. An underwater acoustic locator receiver (model N15A235B, Dukane Corp, St. Charles, Illinois, USA) was used to facilitate recapture of tagged animals both from the boat and underwater.

Five records of diving behavior were obtained through the recapture of TDR equipped immature hawksbills. During the deployment of TDR-1 on one turtle the unit suffered battery depletion causing the corruption of a large part of the dive information. We failed to recapture an additional animal (carrying TDR-2) by the end of the research period. Data for both these turtles are not presented here. Usable time-depth records were obtained from four turtles, yielding continuous behavioral records of between 10.9 and 11.8 days duration (Table 1).

Surveys to measure the extent and distribution of feeding scars on sponges were conducted along two approximately 240 m long segments of cliff wall at the study site. The number of feeding scars were counted independently by two SCUBA equipped observers for bands 5 m in vertical extension and centered upon the 20, 15, 10, and 5 m isobaths. Counts along the wall from the surface to 2.5 m depth were made by swimming with snorkeling equipment.

## Results

The four instrumented hawksbills exhibited remarkably similar patterns of diving and surfacing behavior. The dive and surfacing information collected for each turtle is summarized in Table 2. Any submergence exceeding one meter in depth was considered a dive. While turtles exhibited considerable variation in the number of dives made per day, differences in the average number of daily dives were not significant between the records for each of the animals (pairwise Mann-Whitney U-tests;  $P > 0.001$ ).

### Foraging and resting dives

Fig. 2 chronicles the diving behavior of hawksbill 93-053 for a 24 hr period. The behavioral pattern appears typical of most conduct recorded for the four turtles and comprises two markedly different dive types. From 06:34 to 11:56 hrs and again from 14:56 to 16:47 hrs on 23 October turtle 93-053 made movements resulting in continuous depth fluctuations throughout each submergence interval. We call these submergences "foraging dives" and these dives are labeled as such in Fig. 2. Dives with little change in measured depth other than variation

attributable to wave action or breathing episodes are called "resting dives" (the unlabeled dives in Fig. 2).

Activity in the hawksbills examined had a strong diurnal component (Fig. 3). Periodic bouts of foraging dives were made for a mean of 8.4 hrs per day, mostly during daylight hours. The immature turtles spent an average of 3.6% time at the surface during the mean daytime period (from 06:30 to 18:30 hrs), whereas surfacing time was reduced to 1.8% at night when turtles were largely inactive.

#### Dive duration and surface intervals

Immature hawksbill dives lasted on average 19.0 min and surface intervals were of 32.9 s mean duration. Partitioning of the data according to dive type exposes profound differences in the properties of foraging and resting dives (Table 3). For each of the turtles, foraging dives were of significantly shorter duration (Fig. 4) and had shorter post-dive surface intervals than resting dives (one tailed t-tests, assuming independence of samples;  $P < 0.001$ ). Correlations between dive duration and post-dive surface interval were significant for foraging dives in all turtles ( $0.307 \leq r \leq 0.528$ , Pearson product moment;  $P < 0.001$ ), yet generally weaker and not consistently significant for resting dives ( $0.098 \leq r \leq 0.308$ ). The duration of resting dives increased steadily on average for 8 hours after the onset of dusk (Fig. 5; data pooled for all turtles).

Correlations of turtle size (straight carapace length) with duration of foraging dives were strong and significant ( $r = 0.951$ ;  $P < 0.001$ ), while no such significant trend was evident in length of the resting dives. However, post-resting dive surface intervals did correlate significantly and positively ( $r = 0.8843$ ;  $P < 0.001$ ) with turtle size. The highly variable post-surface intervals of foraging dives exhibited no significant size-related trends.

#### Dive depth

Mean depth of foraging dives was significantly less than of resting dives in three out of four turtles (Table 3; pairwise Mann-Whitney U-tests;  $P < 0.001$ ; exception: turtle no. 94-085). Fig. 6 illustrates the depth distribution of foraging and resting dives; overall mean foraging dive depth was 4.7 m, while resting dives had a mean depth of 6.8 m. Foraging dive durations increased significantly with dive depths ( $r = 0.1384$ ; Pearson product moment;  $P < 0.001$ ), but resting dive durations did not. Post-dive surface intervals were positive but weakly correlated with dive depth (foraging dives:  $r = 0.1186$ , resting dives:  $r = 0.0699$ ;  $P < 0.001$ ). Turtle size correlated significantly and positively with foraging dive depth ( $r = 0.898$ ;  $P < 0.001$ ), but differences in resting dive depth were not attributable to turtle size.

The dive records did not uniformly correspond to the pattern of alternating bouts of short, shallow foraging dives and longer, deeper resting dives. Fig. 7 depicts an example of deviations from the typical behavioral pattern by turtle no. 94-085, the largest hawksbill examined. The animal made three dives that were deeper and of longer duration than usual for foraging dives. While post-dive surface intervals were not notably longer than normal, the turtle did spend an unusual amount of time at the surface immediately prior to the dives (72, 128 and 144 s respectively).

Horizontal turtle movement along the cliff wall as measured by the distance between TDR deployment and recovery capture locations varied strongly (from 0.1 to 2.0 km) between individuals. Dives of turtles beyond 34 m, the maximum depth of the cliff base, indicate movements away from the cliff wall. The dive depths of up to 72 m, provide evidence of excursions by the animals to waters several hundred meters away from the cliff wall.

#### Prey sponge distribution

Densities of feeding scars on encrusting sponges surveyed along the cliff wall were high in the uppermost zone (from the surface to 2.5 m depth) and declined strongly at greater depth (Table 4). The observed scars were characteristic of those caused by hawksbill feeding on sponges. Hawksbill feeding behavior in shallow water was observed by us on several occasions within the study area.

#### Discussion and conclusions

Foraging patterns of immature hawksbills are similar to those observed for juvenile green turtles by Ogden et al. (1983) and Bjorndal (1980), with feeding bouts during daylight hours and resting behavior predominant at night. We found hawksbill daytime dive durations were mostly longer than the 3 to 10 min reported for Chelonia (size: 7 to 8 kg) on shallow seagrass beds (Ogden et al., 1983).

#### Feeding, predator avoidance and resting behavior

The recorded dive profiles represent the vertical component of excursions by turtles surfacing for respiration, foraging, resting, and/or predator avoidance. Hawksbills along Mona Island's cliff wall are presented with a range of depth options and can make dives down to 34 m water depth without expending effort in horizontal movement. However, the vast majority of dives made by the turtles involve depths of 7 m or less (see Fig. 6). Given that the shallowness of foraging dives corresponds well with the distribution of feeding scars on encrusting sponges, most of which are found in the upper few meters along the wall, we feel confident in our judgment that most dives labeled foraging dives indeed involve feeding or prey searching behavior. However, occasional foraging dives of turtles to deeper water are likely to reflect other behaviors, such as predator avoidance or exploration. Large fish are potential predators of hawksbills (e.g. Galeocerdo cuvier (Randall, 1967) and Epinephelus itajara (Cadenat 1957)) and typically swim parallel to the cliff wall. Turtles may successfully evade these predators by descending to the cliff base and moving away from the wall to deeper water. This evasive behavior was frequently observed by us in our attempts to capture cliff wall turtles and many escaped using this maneuver. In contrast, a few deep dives appear preplanned, such as those to depths greater than 50 m illustrated in Fig. 7, and are not likely made in response to immediate external threats. These dives reflect purposeful behavior by the turtles requiring substantial effort for which the objectives remain unclear.

Turtles making resting dives on perches near the surface risk being dislodged by water motion caused by waves colliding with the cliff wall. The majority of resting dives were made to depths of 2 to 7 m and these depths probably represent

compromises by the animals aimed at minimizing disturbance by wave action and minimizing surfacing effort by staying in shallower water. Turtles made an average of 16 to 31 trips to and from the surface per day between resting dives and any decrease in dive depth would substantially reduce surfacing effort. Avoiding lung collapse to retain access to the lung oxygen store and allowing the turtles to prolong bottom times may be another incentive for resting in shallow waters.

#### Oxygen stores and metabolic rates

The mean duration of hawksbill resting dives observed by us fall in the range of resting and night dive durations noted by Parrish (1958) for an assembly of chelonid turtles (including Eretmochelys) held in tanks 5.5 m and shallower. Markedly longer durations of foraging dives in wild hawksbills as compared to those observed in captive marine turtles may be attributed to greater environmental challenges and resulting physical conditioning faced by the former. Interestingly, the hawksbill dives along the cliff wall of longer than normal duration were mostly deep dives (for example, see Fig. 7), during which the lung oxygen store may be less available due to lung collapse.

In a study by Lutz and Bentley (1985) of captive loggerhead turtles, the lung was determined to be the principal oxygen store for diving. The hawksbills we studied, while extending surface intervals after long and deep dives, often made longer than normal surfacings prior to these dives, suggesting the animals anticipated the extent of the dives and hyperventilated to store oxygen in tissues other than the lungs. Further evidence in support of the hypothesis that these turtles other tissues are used to store oxygen is offered by the observations of Kontos and Eckert (1988) who watched hawksbills surface along the cliffs of Mona Island. They found that juvenile and adult hawksbills took 3.51 and 5.85 breaths per surface interval, respectively. Such a respiratory pattern seems excessive for the mere repletion of oxygen in the lung when the tidal volumes of turtles are greater than 50% of lung capacity (measured for Chelonia mydas by Tenney et al., 1974). Instead, hawksbill turtles probably utilize and recharge substantial oxygen stores in blood and muscle tissues during their routine diving cycles, as do most diving birds and marine mammals (Kooyman, 1989).

Although we found a correlation between foraging dive duration and the subsequent surface interval, surfacings after prolonged, deep foraging dives were not of dramatically increased duration. This indicates that it is improbable that anaerobic metabolic pathways were used during the dives. Green turtles in forced diving experiments have been shown to require long (>10 hr) recovery periods to reduce lactic acid accumulations (Berkson, 1966). Results supporting our observations were obtained for captive, 10-20 kg loggerheads by Lutcavage and Lutz (1991). They concluded that the loggerheads were capable of making aerobic dives of  $\leq 1$  h.

The significantly longer duration of resting submergences compared with foraging dives is attributable to lowered metabolic requirements when resting. Measurements of metabolic rates in juvenile green turtles by Prapge (1976) demonstrate that at rest these turtles had rates up to four times lower than when swimming. The variation in nocturnal dive durations (Fig. 5) provides clues as

to the dynamics of metabolic rates in hawksbills at rest. Assuming that we may use resting dive duration as an inverted gauge of metabolic rate, the duration increases indicate that turtle metabolic rates fell continuously for 8 hrs after the onset (at dusk) of resting dive sequences.

The cliff walls of Mona Island constitute an important developmental habitat for a wide size range of immature hawksbills. Because turtles appear able to find adequate food and shelter in the upper few meters of the sublittoral zone, little incentive exists for the hawksbills to make deep, prolonged dives that would approach their physiological limitations. Further investigations, both in the field and in the laboratory, should improve our understanding of the limitations and metabolic scope of breath-hold diving in these turtles.

#### Acknowledgements

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#### FIGURE LEGENDS

Fig. 1. (a) Study area (arrows) at the cliff-walls Mona Island, (b) Cross-sectional diagram of the cliff-wall hawksbill habitat.

Fig. 2. Eretmochelys imbricata. Diving in the 32.1 cm (straight-line carapace length) hawksbill 93-053 during a 24 hr segment starting on 23 October 1994 at 06:00 hrs. Submergences exhibiting continuous variation in measured depth throughout the dive are labeled "foraging" dives. Descents marked by an asterisk (\*) appear related to finding the habitual resting site.

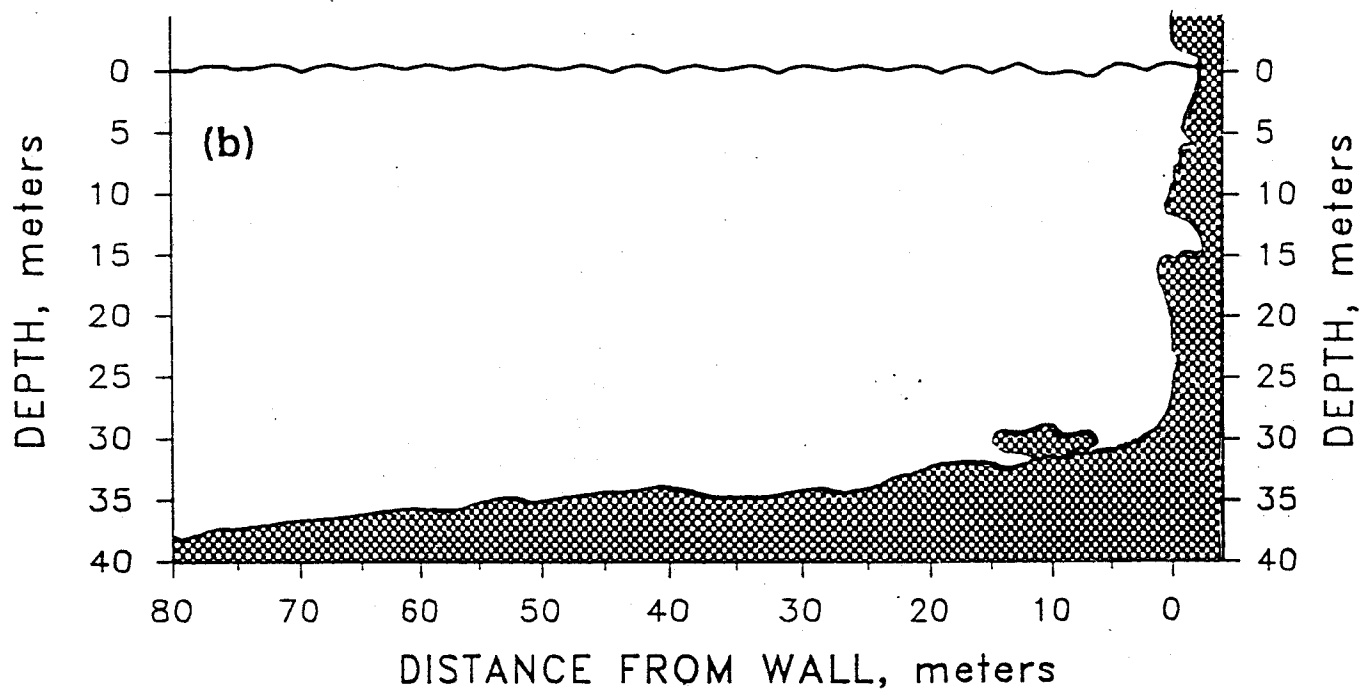
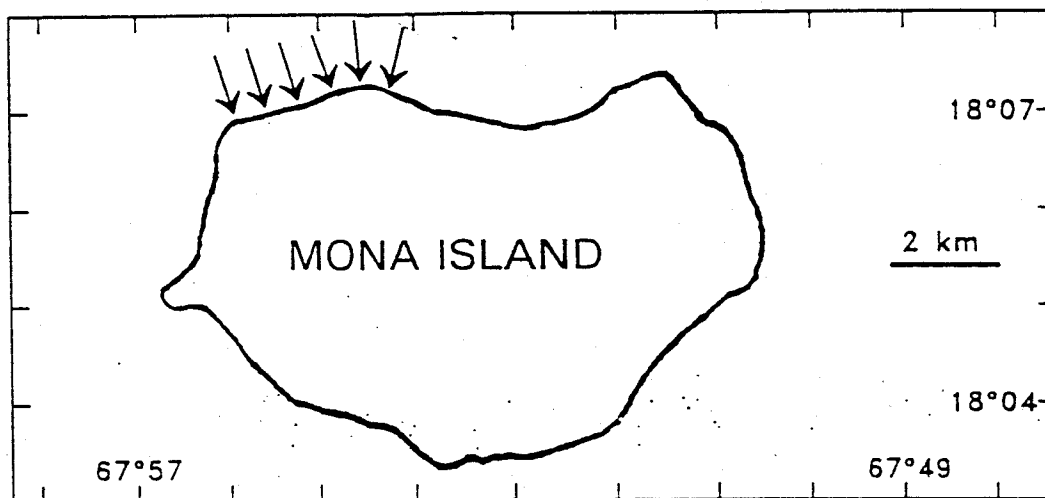
Fig. 3. Eretmochelys imbricata. Diel behavioral pattern as recorded in four immature hawksbills. Percent time turtles spent during surfacings, resting and foraging dives are presented in twenty-four 1-hr segments. The daylight period during the study extended from 06:00-6:30 to 18:15-19:00 hrs local time.

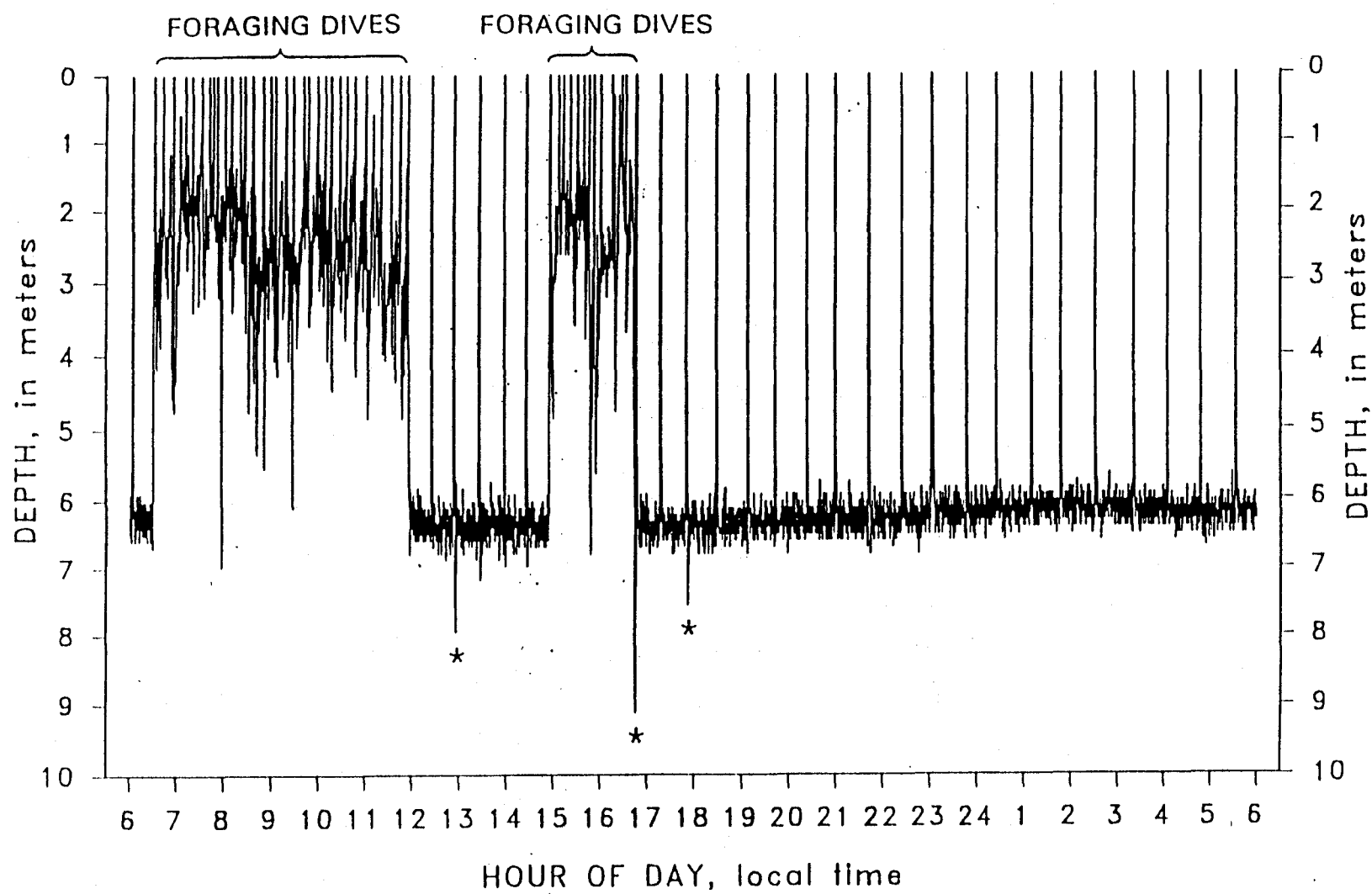
Fig. 4. Eretmochelys imbricata. Dive duration distribution in minutes of 2136 foraging and 1217 resting dives as proportion of all dives made by four immature hawksbills.

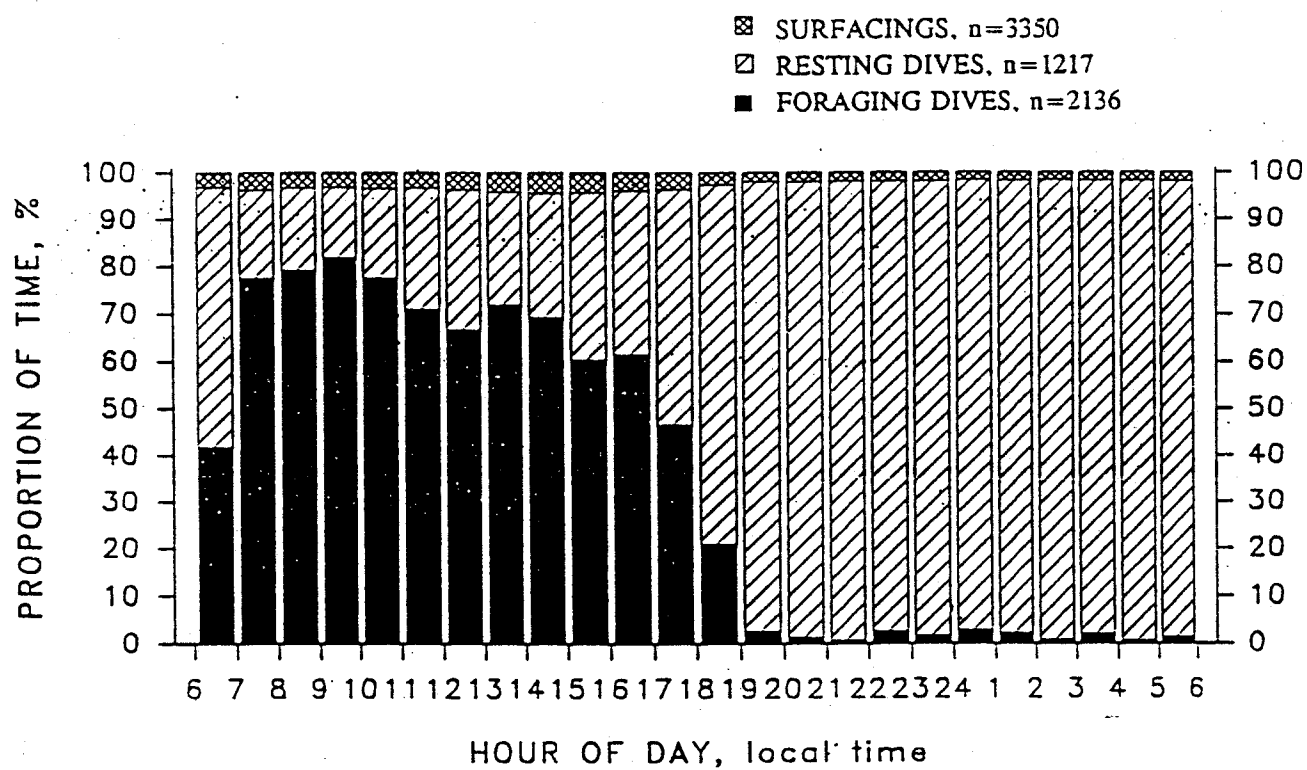
Fig. 5. Eretmochelys imbricata. Mean duration ( $\pm$  standard deviation) for a total of 887 nightly resting dives by hourly interval. Time at midpoint of dive determined the dives entered for each of the hourly means calculations.

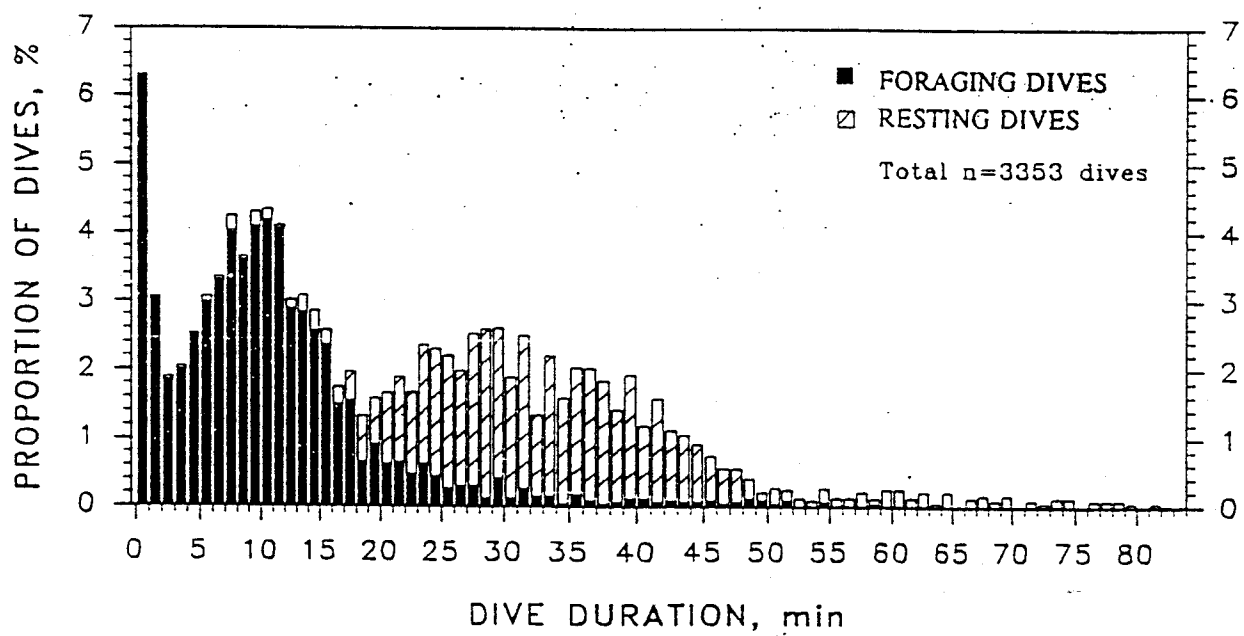
Fig. 6. Eretmochelys imbricata. Mean depth distribution in meters of 2136 foraging and 1217 resting dives as proportion of all dives made by four immature hawksbills. Means per dive were calculated as average depth during the submergence interval, including surfacing descents and ascents.

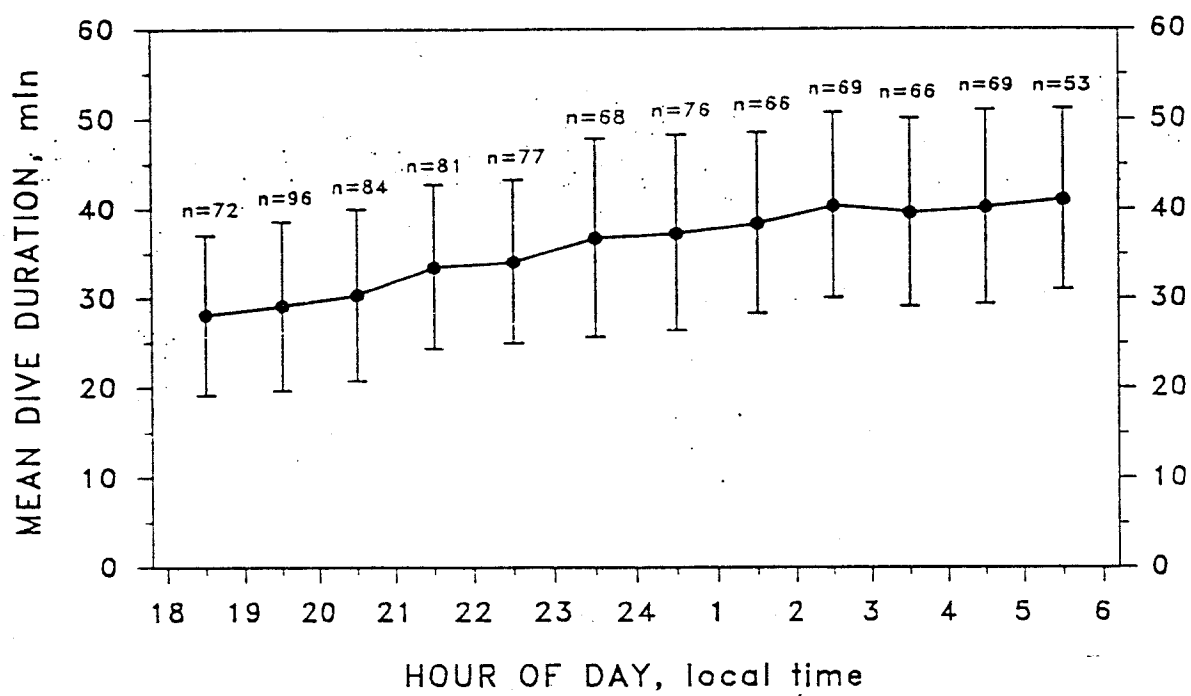
Fig. 7. Eretmochelys imbricata. Diving in the 53.4 cm (straight-line carapace length) hawksbill 94-085 during a 6 hr period starting on 27 August 1994 at 06:30 hrs. The turtle made three dives (starting at 8:30, 10:58 and 11:53 hrs) exceeding 50 m in depth. Note the prolonged surfacing (marked with \*) prior to each of these deep foraging dives, suggesting the turtle anticipated the extent of the dives.

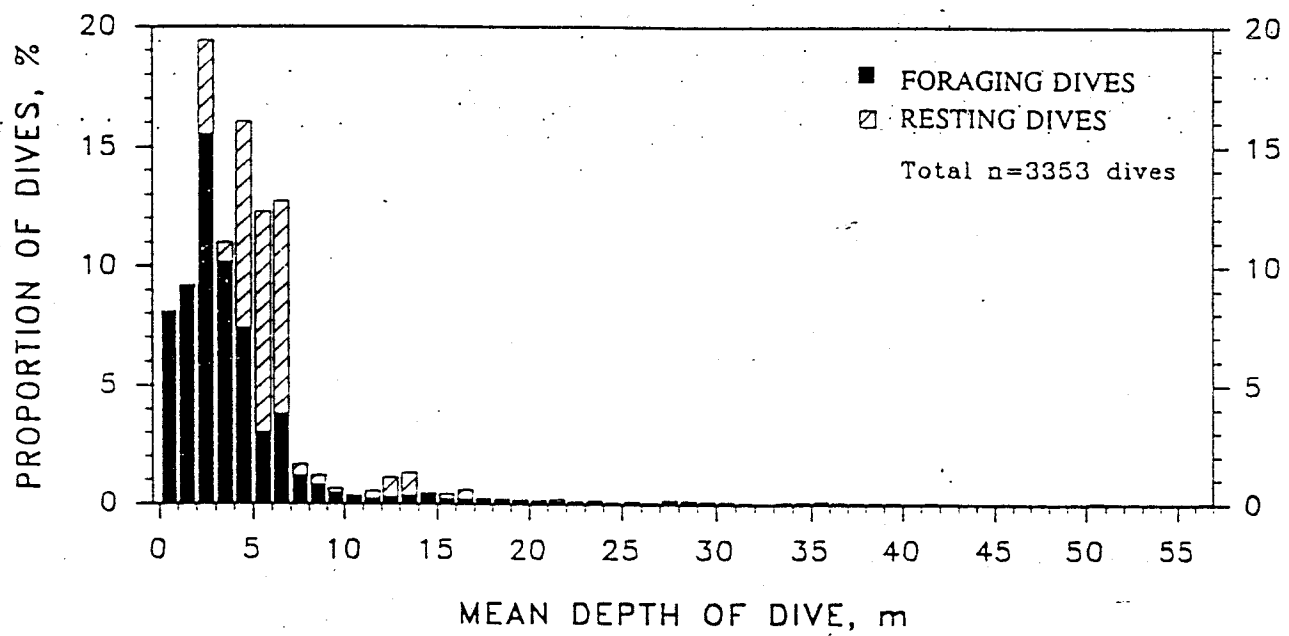












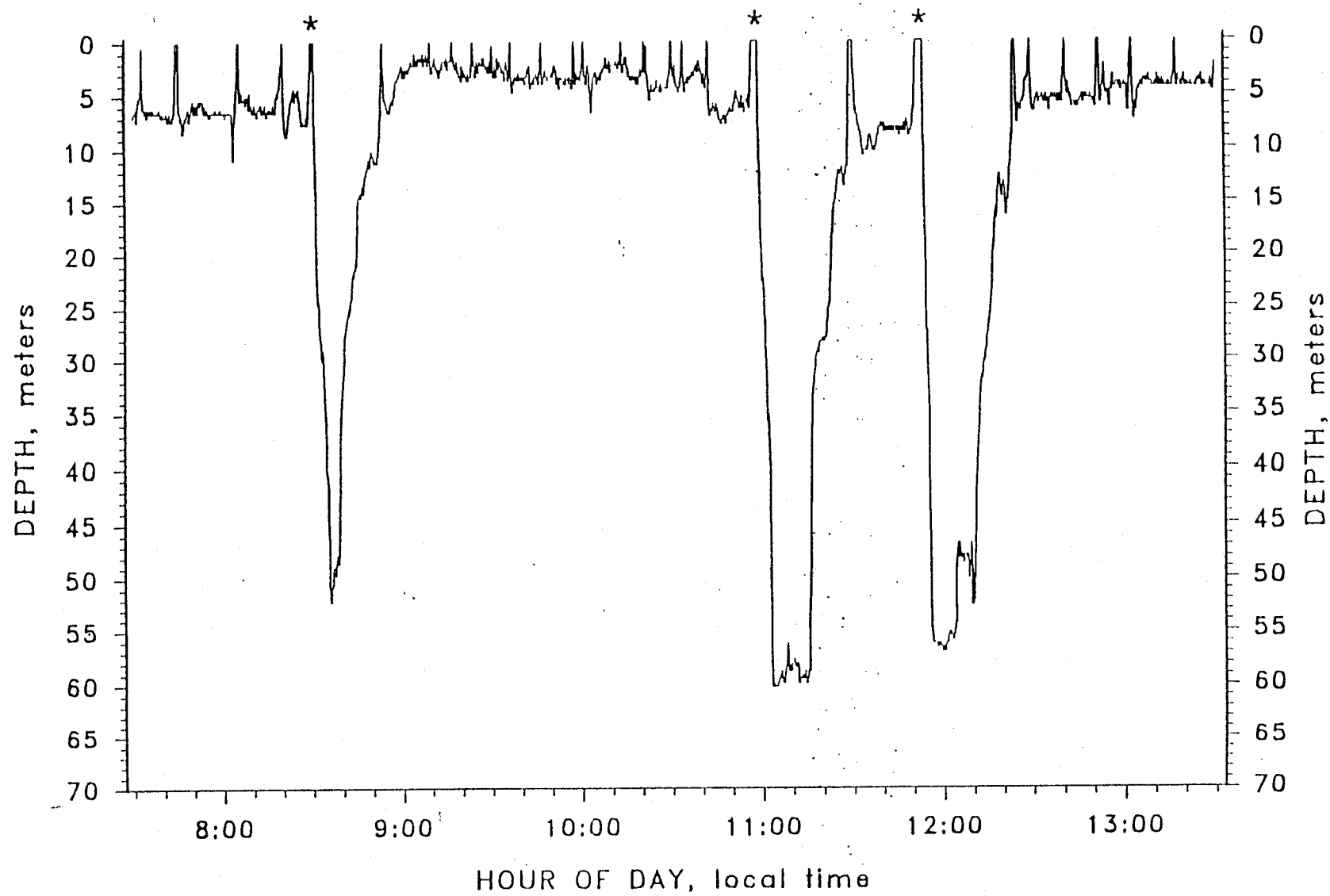


Table 1. Eretmochelys imbricata. Biological and experimental data of four time-depth recorder (TDR) equipped immature hawksbill sea turtles. Turtle behavior was monitored continuously from the time of instrument deployment. Distance moved is the distance between the instrumented turtle release site and location of recapture. The experiment was conducted during 1994 along the northwest coast of Mona Island, Puerto Rico.

| Turtle no. | Straight-line<br>carapace<br>length (cm) | Body mass<br>(kg) | Instrument<br>deployed | Date and time<br>of instrument<br>deployment | Date and time<br>of instrument<br>recovery | Length of<br>behavioral<br>record (d) | Distance moved<br>(km) |
|------------|------------------------------------------|-------------------|------------------------|----------------------------------------------|--------------------------------------------|---------------------------------------|------------------------|
| 94-038     | 32.0                                     | 3.7               | TDR-1                  | 19 August<br>16:42                           | 5 September<br>15:00                       | 11.8                                  | 1.98                   |
| 93-053     | 32.1                                     | 3.8               | TDR-1                  | 16 October<br>16:06                          | 4 November<br>11:45                        | 11.8                                  | 0.86                   |
| 94-041     | 50.5                                     | 16.2              | TDR-1                  | 4 October<br>12:35                           | 15 October<br>10:29                        | 11.0                                  | 1.02                   |
| 94-085     | 53.4                                     | 17.2              | TDR-2                  | 25 August<br>17:20                           | 5 September<br>16:10                       | 10.9                                  | 0.11                   |

Table 2. Eretmochelys imbricata. Summary of the extent of diving in four immature hawksbills at the northwestern cliffs of Mona Island.

| Turtle no. | Number of recorded dives | Dives per day<br>mean $\pm$ SE<br>min - max | Surface interval<br>(s)<br>mean $\pm$ SE<br>min - max | Dive duration<br>(min)<br>mean $\pm$ SE<br>min - max | Dive depth<br>(m)<br>mean $\pm$ SE |
|------------|--------------------------|---------------------------------------------|-------------------------------------------------------|------------------------------------------------------|------------------------------------|
| 94-038     | 971                      | 82.1 $\pm$ 0.9<br>49 - 159                  | 22.1 $\pm$ 0.4<br>8 - 80                              | 17.1 $\pm$ 0.4<br>0.1 - 57.7                         | 3.1 $\pm$ 0.1                      |
| 93-053     | 901                      | 77.7 $\pm$ 1.8<br>25 - 208                  | 33.0 $\pm$ 0.6<br>8 - 136                             | 18.3 $\pm$ 0.6<br>0.1 - 81.1                         | 5.5 $\pm$ 0.2                      |
| 94-041     | 714                      | 63.3 $\pm$ 0.7<br>26 - 84                   | 38.3 $\pm$ 0.7<br>8 - 152                             | 21.4 $\pm$ 0.5<br>0.1 - 78.0                         | 5.2 $\pm$ 0.2                      |
| 94-085     | 767                      | 71.3 $\pm$ 0.5<br>46 - 94                   | 41.4 $\pm$ 0.9<br>8 - 184                             | 19.9 $\pm$ 0.4<br>0.1 - 52.0                         | 5.4 $\pm$ 0.2                      |

Table 3. Eretmochelys imbricata. Summary of immature hawksbill diving data after partitioning into "foraging" and "resting" dives (for separation criteria, see text).

|                | Turtle<br>no. | n   | Post-dive surface<br>interval (s)<br>mean $\pm$ SE<br>min - max | Dive duration<br>(min)<br>mean $\pm$ SE<br>min - max | Dive depth<br>(m)<br>mean $\pm$ SE | Maximum depth<br>recorded (m) |
|----------------|---------------|-----|-----------------------------------------------------------------|------------------------------------------------------|------------------------------------|-------------------------------|
| FORAGING DIVES | 94-038        | 639 | 18.4 $\pm$ 0.5<br>8 - 56                                        | 8.9 $\pm$ 0.3<br>0.1 - 35.6                          | 2.7 $\pm$ 0.1                      | 27.3                          |
|                | 93-053        | 596 | 29.5 $\pm$ 0.8<br>8 - 136                                       | 8.6 $\pm$ 0.4<br>0.1 - 54.9                          | 3.7 $\pm$ 0.2                      | 34.3                          |
|                | 94-041        | 451 | 34.2 $\pm$ 0.8<br>8 - 112                                       | 14.0 $\pm$ 0.4<br>0.1 - 58.9                         | 4.7 $\pm$ 0.3                      | 44.2                          |
|                | 94-085        | 450 | 31.9 $\pm$ 1.1<br>8 - 184                                       | 12.5 $\pm$ 0.4<br>0.1 - 52.0                         | 6.4 $\pm$ 0.3                      | 72.1                          |
| RESTING DIVES  | 94-038        | 332 | 29.3 $\pm$ 0.7<br>8 - 80                                        | 33.1 $\pm$ 0.5<br>2.7 - 57.7                         | 4.0 $\pm$ 0.1                      | 32.6                          |
|                | 93-053        | 305 | 39.7 $\pm$ 0.9<br>8 - 88                                        | 37.1 $\pm$ 0.9<br>11.2 - 81.1                        | 9.1 $\pm$ 0.3                      | 37.5                          |
|                | 94-041        | 263 | 45.4 $\pm$ 1.1<br>8 - 152                                       | 33.9 $\pm$ 0.7<br>10.9 - 77.5                        | 6.0 $\pm$ 0.2                      | 31.1                          |
|                | 94-085        | 317 | 54.9 $\pm$ 1.0<br>8 - 104                                       | 30.4 $\pm$ 0.5<br>9.7 - 50.1                         | 6.2 $\pm$ 0.2                      | 56.2                          |

Table 4. Results of a feeding scar survey performed along the cliff wall (A) east of Esperanza cave and (B) east of Espinal cave, Mona Island. Horizontal extension of both surveyed areas is approximately 240 m. The base of the cliff wall lies at between 24 and 28 m depth for area A and between 16 and 25 m depth for area B. Observers were RVD and CED.

|   | Survey zone<br>depth (m) | Number of observed<br>feeding scars (RVD/CED) | Mean feeding scar<br>density (m <sup>-2</sup> ) |
|---|--------------------------|-----------------------------------------------|-------------------------------------------------|
| A | 0 - 2.5                  | 208 / 130                                     | 0.282                                           |
|   | 2.5- 7.5                 | 44 / 61                                       | 0.044                                           |
|   | 7.5-12.5                 | 9 / 12                                        | 0.009                                           |
|   | 12.5-17.5                | 4 / 1                                         | 0.002                                           |
|   | 17.5-22.5                | 7 / 4                                         | 0.005                                           |
| B | 0 - 2.5                  | 154 / 130                                     | 0.237                                           |
|   | 2.5- 7.5                 | 85 / 45                                       | 0.054                                           |
|   | 7.5-12.5                 | 15 / 26                                       | 0.017                                           |
|   | 12.5-17.5                | 3 / 2                                         | 0.002                                           |