

## Observations on sea turtles at Aldabra Atoll

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[Plates 26 to 29]

This paper is a preliminary report based on observations made from January to July 1968 and on expedition notes from August 1967 to November 1968. The majority of the work was carried out on adult green turtles which had been harpooned and captured by the Seychellois turtlemen at Aldabra. A small number of observations were made on nesting females and hatchlings of the same species.

Males are, on average, smaller than females; this is the reverse of the expected situation and may be due to the fact that more males than females are captured. The relevance of various body proportions is discussed, as are the results of regression analysis of the measurements.

Coloration of the adult carapace is extremely variable, but certain colour characteristics are strongly correlated with sex; a predictive index for sex determination is presented.

Green turtles at Aldabra have similar breeding biology to other populations.

Hatchling and egg measurements reflect the same trends shown by the adult females.

A number of different organisms were found on adult green turtles: barnacles, leeches, isopods, green algae, and red algae. In addition, tabanids and mosquitoes were found on turtles above water. Sharks and ghost crabs are probably important predators of adults and young respectively. Only one internal parasite was found.

Incidental observations were made on hawksbills. The first recorded specimen of a loggerhead from Aldabra was obtained. Information from Seychellois turtlemen relating to sea turtles at Aldabra is presented; economic importance and problems of conservation are raised.

### 1. INTRODUCTION

Aldabra Atoll is important to sea-turtle studies for two reasons: it is a main centre for green turtle breeding in the Western Indian Ocean (Parsons 1962, p. 47), and it is the home of a light shelled, 'blonde', race of hawksbill (Hornell 1927, p. 10). However, very little turtle research has been carried out on this atoll, and it is the purpose of the present paper to amalgamate sea-turtle information from this area, to assess its importance in the light of findings from other localities, and, finally, to draw attention to some further problems.

The first accounts of sea turtles in the Aldabra area make reference to the removal and slaughter of incredibly large numbers of animals in the late nineteenth century (see Parsons 1962, p. 47). The first really informative account seems to have been made by Spurs (1892) whose ideas are consistent with some of today's most up-to-date theories. Later accounts (A. Voeltzkow 1897; S. Voeltzkow 1913; Fryer 1911; Krümmel 1912; Wheeler 1953) contain information only of general interest. cursory popular accounts will be found in Ommanney (1949), Cousteau (1963), and Travis (1959). Two recent typescripts (Gaymer 1966, Veevers-Carter 1962) contain a small amount of information. Measurements and observations from brief visits will be found in Hirth (F.A.O. 1967) and Honegger (1967).

By far the most comprehensive work on sea turtles in the Seychelles administrative area (which includes Aldabra) is that of Hornell (1927), and, although he does not quantify many points, he brings together a great deal of information.

Most work on sea turtles from this area deals with the green turtle, for this is the most important species to the Seychellois, both as a source of income and as a source of food. Also, this

species has occurred in relatively large numbers so that many have been captured and hence have been available for study. The hawksbill, on the other hand, occurs in smaller numbers in the Aldabra area and is less in demand, consequently fewer specimens are available for study. Past records of other species in this area are unsubstantiated with specimens.

## 2. MATERIALS AND METHODS

### (a) *Green turtle*

Three subadult and 158 adult green turtles were examined on Aldabra; the majority of these animals had been captured by the Seychellois turtlemen. Of eleven nesting females, nine were tagged; another animal, harpooned and then released by the Seychellois, was also tagged. In addition, two females were examined at Menai Island, Cosmoledo. Eighty-three hatchlings from five different clutches and twelve eggs from one clutch were examined.

Skulls found lying about on the atoll were collected and examined; 65 turtles were examined in detail for epizotic symbionts; four animals were examined for internal parasites; stomach contents of five animals were collected and analysed; and a small amount of material for histological examination was collected.

### (b) *Hawksbill*

Five specimens of this species were examined on Aldabra; stomach contents from one were collected.

### (c) *Loggerhead*

One specimen of this species was collected; another, not seen by myself, was reported.

### (d) *General*

Epidermal and osteological terms are as in Carr (1952). The measurements taken include:

- carapace straight length—the straight line distance along the midline of the carapace from its most anterior edge at the precentral scale to its most posterior edge at the post-central scale (measured with wooden dividers).
- carapace curved length—the distance along the curve of the carapace between the above mentioned points (measured with a tape).
- carapace straight width—the greatest straight line distance perpendicular to the long axis of the body taken between two corresponding marginals—usually the sixth pair (measured with wooden dividers).
- carapace curved width—the distance over the curve of the carapace between the above mentioned points (measured with a tape).
- plastron length—the straight line distance taken along the midline between the anterior edge of the plastron (intra-gular) and the posterior edge of the plastron (intra-anal) (measured with wooden dividers).
- head width—the greatest width of the head taken before the temporals.

Measures for adults are in centimetres; those for hatchlings and eggs in millimetres.

Relevant material was examined at the British Museum (Natural History) and the Oxford University Museum.

Information regarding sea turtles from the Seychelles area was received from the following: American Museum of Natural History, Florida State Museum, United States National Museum,

Museum of Comparative Zoology (Harvard University), City of Liverpool Museum, City Museum (Bristol), Muséum National d'Histoire Naturelle (Paris), Natur-Museum und Forschungs-Institut Senckenberg (Frankfurt), Western Australian Museum.

### 3. GREEN TURTLE *CHELONIA MYDAS* L.

'The greatest concentration of breeding turtles in the Indian Ocean in modern times, and perhaps in antiquity, has been at the raised atoll of Aldabra and the adjacent smaller islands of Assumption and Cosmoledo [*sic* and Astove], which together comprise the Aldabra group, politically appendages of the British colony of Seychelles since 1810'; it is with these words that Parsons (1962, p. 47) begins his discussion of the green turtles of Aldabra. And, indeed, the figures referring to the early exploitation of turtles from Aldabra are quite astounding. Spurs in 1892 predicted that some 12000 turtles would be captured in one year at Aldabra; Hornell (1927, p. 27) relates accounts of 200 and 300 animals being turned in a *single night* on Assumption.

In recent times the annual export from Aldabra has been roughly 500. This depressing decline in numbers of green turtles has triggered off a number of studies into the biology of this animal at Aldabra. Nevertheless, as will become apparent, our information is still very incomplete and at a very preliminary stage.

#### (a) *Occurrence and breeding season*

Hornell (1927, p. 37) mentions that green turtles are found at Aldabra in all months of the year; he produces evidence of this in the form of records of catches from Aldabra and Assumption (pp. 32 and 33). From this information he concludes that the 'true laying season extends from February to September inclusive'; he also feels that this period consists of two overlapping breeding seasons of two separate populations—one from February to May and the other from May to September (p. 37). The only other locality where breeding is known to go on all the year round is Sarawak (Parsons 1962), and it too has a definite breeding peak (Hendrickson 1958).

Observations by expedition personnel from August 1967 to November 1968 (table 1) confirm that turtles breed at Aldabra round the year. It also appears as if there is a distinct peak in laying from February to July—consistent with Hornell's timetable. It must be emphasized that the number of observers and observer times were not constant from month to month so that the differences between months could be due to an observation bias. I can see no evidence in either Hornell's data (1927, pp. 32, 33) or the present data to suggest that two distinct populations are breeding at different times at Aldabra. (See Adult measurements §3g).

Sightings of green turtles were made from all major camp sites (Anse Cèdres, Cinq Cases, Dune Jean-Louis, Dune d'Messe, and Anse Mais) and from other localities right round the atoll (figure 1). There is only one record from the lagoon, indicating that this species rarely occurs there.

#### (b) *Mating*

The only sighting of copulating turtles in the lagoon was from Bras Cinq Cases, reported by P. Grubb (personal communication). Eleven other sightings were from outside the atoll; of these, ten were between the shore and the reef and only one from outside the reef. Seven of eleven sightings were made before midday (and two others were made shortly after).

These findings are consistent with those by Hendrickson (1958, p. 482), who found most

TABLE 1. GREEN TURTLE BREEDING ACTIVITY

Number of nests per month at various beaches

| beach               | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov.  | Dec. | total nests | pits | all activity total |
|---------------------|------|------|------|------|-----|------|------|------|-------|------|-------|------|-------------|------|--------------------|
| Settlement          | —    | —    | 1    | 1    | 1   | 1    | —    | —    | —     | —    | —     | —    | 4           | 0    | 4                  |
| Anse Var            | —    | —    | —    | —    | —   | —    | —    | —    | —     | —    | —     | —    | 0           | 2    | 2                  |
| Anse Polymnie       | —    | —    | —    | —    | —   | —    | —    | —    | —     | —    | —     | —    | 0           | 10   | 10                 |
| Anse Coco           | —    | —    | —    | 1    | —   | —    | —    | —    | —     | 1    | —     | —    | 2           | 0    | 2                  |
| Anse Porche         | —    | 1    | —    | —    | —   | —    | —    | —    | —     | 3    | —     | —    | 4           | 0    | 4                  |
| Anse Malabar (west) | —    | —    | 3    | —    | —   | —    | —    | —    | —     | —    | —     | —    | 3           | 12   | 15                 |
| Anse Malabar (east) | —    | —    | 8    | 1    | —   | 1    | 6    | —    | ×     | —    | 1H    | —    | 18          | 40   | 58                 |
| Anse Badamier       | —    | —    | 1    | —    | —   | —    | 1    | —    | —     | —    | 1     | —    | 3           | 7    | 10                 |
| Anse Cèdres         | 3H   | —    | —    | —    | ×   | 8    | H    | —    | ×××   | —    | 1HHH× | —    | 17          | 30   | 47                 |
| North Cinq Cases    | —    | —    | —    | —    | —   | —    | —    | —    | —     | —    | —     | —    | 0           | 30   | 30                 |
| Cinq Cases          | —    | —    | —    | —    | —   | 4    | —    | —    | —     | —    | —     | —    | 4           | 30   | 34                 |
| South Cinq Cases    | 1    | —    | 1    | —    | —   | —    | —    | —    | —     | —    | —     | —    | 2           | 4    | 6                  |
| Anse du Bois        | —    | 1    | —    | —    | —   | 2    | 1    | —    | —     | —    | —     | —    | 4           | 11   | 15                 |
| Anse Bigo           | —    | —    | —    | 1    | —   | —    | —    | —    | —     | —    | —     | —    | 1           | 0    | 1                  |
| Dune Y              | —    | 3    | —    | 1    | 3   | —    | 1    | —    | —     | —    | —     | —    | 8           | 12   | 20                 |
| Dune Z              | —    | 2    | —    | —    | —   | 1    | 2    | —    | —     | —    | —     | —    | 5           | 10   | 15                 |
| Dune Jean-Louis     | —    | 3HH  | —    | 1×   | 3×  | 4H   | 3H   | —    | —     | —    | —     | ×    | 18          | 30   | 48                 |
| Dune au Pic         | —    | —    | 1    | —    | —   | —    | 2    | —    | —     | —    | —     | —    | 3           | 35   | 38                 |
| Entreboy            | —    | —    | 1    | —    | —   | —    | —    | 2    | —     | —    | —     | —    | 3           | 50   | 53                 |
| 'Anse Mais'         | —    | —    | —    | —    | —   | —    | ×    | —    | 3H    | —    | —     | —    | 4           | 0    | 4                  |
| total nesting       | 4    | 10   | 16   | 7    | 9   | 21   | 17   | 2    | 7     | 4    | 4     | 2    | 103         | 313  | 416                |
| in copulation       | 1    | 0    | 2    | 4    | 2   | 0    | 0    | 0    | 0     | 0    | 3     | 0    |             |      |                    |

H, hatchlings recorded; this gives rise to ×, 2 months earlier—i.e. the clutch from which these come. Pits, apparent nests, are added to actual nests to get a crude estimate of nesting activity.

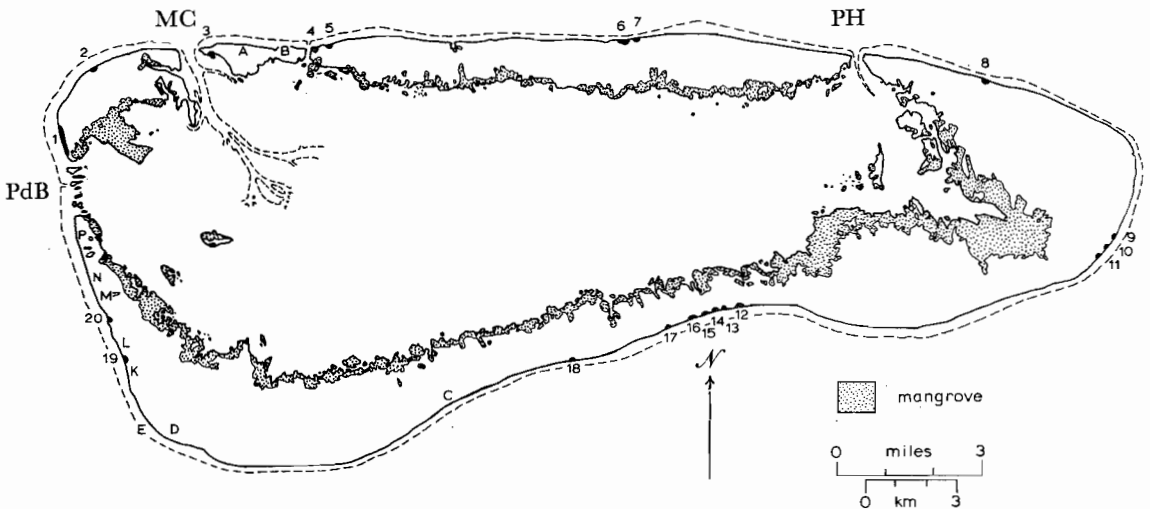


FIGURE 1. Green turtle nesting beaches on Aldabra. Beaches known to have nesting: 1, Settlement; 2, Anse Var; 3, Anse Polymnie; 4, Anse Coco; 5, Anse Porche; 6, Anse Malabar (east and west); 7, Anse Badamier; 8, Anse Cèdres; 9, north of Cinq Cases; 10, Cinq Cases; 11, south of Cinq Cases; 12, Anse du Bois; 13, Anse Bigo; 14, 'Dune Y'; 15, 'Dune Z'; 16, Dune Jean-Louis; 17, Dune au Pic; 18, Entreboy; 19, Anse Mais; 20, north of Anse Mais. Beaches suspected of having nesting: A, Anse Cèdres Polymnie; B, Petit Anse Cèdres Polymnie; C, Anse Quive, D to K, beaches south of Anse Mais (Tambalico, Anse Gilo, Tamarind, Anse Rebise, Anse Badamier, Anse Coco, La Moulroun, De Coco—from south to north); L to N, beaches north of Anse Mais (Trois Cèdres, Anse Gale, De Coco—from south to north); P, Anse Anglais. MC, Main Channel; PH, Passe Houareau; PdB, Passe du Bois.

copulating turtles within 230 m of the shore and most successful copulations between 03h00 and 10h00.

As with nesting, there seems to be a lull in copulation from June to October (table 1). At Tortuguero, Ascension and Sarawak copulation appears to fall off as the breeding season wears on (Carr & Giovannoli 1957, p. 30; Carr & Ogren 1960, p. 15; Carr & Hirth 1962, p. 12; Hendrickson 1958, p. 481). Again, the data in table 1 may be subject to an observer bias from month to month.

There are few accounts of courtship and mating activities in sea turtles, for as Hendrickson (1958, p. 482) has alluded, sharks and currents can often endanger the observer. Attempts to observe copulation from a position in the water at Aldabra were unsuccessful owing to high winds and turbulent water, but brief observations on copulation could be made from the shore. Once mounted, the female paddles with the front flippers and causes the pair to rotate at about one revolution per minute; Hendrickson (1958, p. 484) describes similar small movements of mounted females at Sarawak. When washed close to the rocks it is the female alone who moves the pair away; the male appears unresponsive to the ensuing danger. In one instance the female was able, by frantic efforts, to propel the pair away from the rocks. In another instance—despite the female's efforts—the pair was washed onto some rocks; the male continued to clasp the female until they had actually been stranded and tipped upside down on the rocks. This sequence of events, according to the turtlemen, is not uncommon and may account for a certain amount of adult mortality. This unresponsiveness on the part of the male has been mentioned by Carr & Giovannoli (1957, p. 31), while Carr & Hirth (1962, p. 12) and Hendrickson (1958, p. 484) give evidence of copulating turtles being stranded or washed ashore.

These observations indicate that there must be a tremendous premium on maintaining a clasp on the female. Length of copulation also indicates this; Hendrickson (1958, p. 484) claimed that Sarawak turtles remained in copulation for '20 minutes or more'; Pritchard (1969, p. 95) noted a copulation that lasted at least an hour. Three sightings from Aldabra involved periods of 15, 35, and 65 min. Moorehouse (1933, p. 4) suggested that the pair went to sleep during copulation; this does not appear to be the case at Aldabra where both animals made sporadic breathing movements and the female made light paddling movements.

One important factor selecting for maintenance of the clasp during copulation is competition for females. Numerous authors have described how one female is often surrounded by many vying males (see, for example, Carr 1956; Hendrickson 1958; Hirth in F. A. O. 1967; Spurs 1892; Carr & Giovannoli 1957; Harrison 1954). Hendrickson (1958, p. 483) has described in detail male-male interactions before copulation; Spurs (1892, p. 50) even claimed that 'desperate fights' broke out during the breeding season at Aldabra. Although Hirth (F. A. O. 1967, p. 35; personal communication) indicates that such accumulations of males around a female are not uncommon at Aldabra, there were only three possible sightings of this during the 16 months of observations reported here.

There were several instances of males (?) waiting in the shallows where a female was nesting. This leads to the problem of timing of fertilization which has been raised by numerous authors (Carr & Giovannoli 1957, p. 31; Carr & Ogren 1960, p. 15; Carr & Hirth 1962, p. 12; Carr 1965, p. 82; Harrison 1954; Hendrickson 1958, p. 482). The available data indicate that no one quite knows when a female is most receptive to advances by the male nor what the temporal relation is between copulation, fertilization, and egg-laying. Carr & Ogren (1960, p. 15) suggested that the first mating of a season could occur *after* the female has laid several clutches. This

statement was followed two years later by '...mating brings about fertilization of eggs that will be laid two or three years later and has nothing to do with the eggs of the season' (Carr & Hirth 1962, p. 12). As yet, however, no data have been presented to substantiate this claim.

Two points seem to have prompted Carr to make this suggestion. First, copulations at Tortuguero and Ascension are not seen during the later part of the nesting season. Secondly, during copulation two notches are cut by the male's pollex claws into the anterior marginals of the female's shell. No one knows if this is the rule or the exception but it does happen. Now, it is possible to find females laying early in the season that do not have such notches, and they may acquire notches later on in the season. This indicates that the female may lay several times early in a season without having been fertilized that season. But no one has suggested whether or not these first layings are successful (sea turtles are notorious for laying clutches of 'infertile' eggs—Balasingam 1965, 1967). *If* the eggs are fertile, and *if* the female really has not been fertilized that season then she must have been retaining viable sperm since her last copulation some 2 or 3 years before. The information to date is much too scant and indirect to be able to substantiate these 'ifs'; we simply do not know what the temporal relation is between copulation, fertilization and egg-laying.

If it is as Carr & Hirth have claimed, then there are a number of very large problems that need to be clarified. How does a female manage to maintain viable sperm for several years, to maintain proper temperature, pH, and nutrients for them? Although there are indications that certain reptiles can store sperm (Goin & Goin 1962, p. 108), no one has suggested that this is an obligatory situation. How do virgin females fit into the picture? Is their first migration to the breeding ground merely to be fertilized and not to lay eggs? Carr & Hirth (1962, p. 13) suggest that it is. Why is it adaptive for these females to travel thousands of kilometres to a breeding ground and *not* breed that year? Why is it adaptive for males to travel thousands of kilometres to the breeding ground in order to deposit sperm for three years hence when they could mate at the feeding ground a few months earlier or later? Obviously this problem needs further study.

### (c) *Migration*

A number of authors have suggested that green turtles migrate to the Mozambique Channel when they finish breeding at Aldabra (e.g. Hornell 1927, p. 41). Although this seems very likely, there is no evidence to support (or to reject) this hypothesis. Spurs (1892) has suggested an even more intriguing hypothesis. He claims that males reside at Aldabra throughout their lives; females, on the other hand, stay at the atoll for several years but on reaching maturity disappear; when they finally return they are covered with barnacles which, apparently, are not normally seen at the atoll.

There is scant information to suggest that a resident population may be present at Aldabra. Six unusually small animals have been recorded; two small males from Dune Jean-Louis in late December 1967 (Taylor, personal communication), two females (87 and 84.5 cm straight length of carapace) and one male (88 cm straight length of carapace) from Main Channel, 5 June 1968; and one small animal from the stomach of a tiger shark, 2 August 1968 (Gamble, personal communication). (It must be noted that there is a law forbidding the capture of green turtles less than 30 in (76 cm) long; this would induce a sampling bias causing fewer than the representative number of small turtles to be taken.) The three animals that I examined were clearly subadults; they were all so small that the chances of their belonging to the adult population are improbable (for the *large* female  $p > 0.0005$ ; for the male  $p < 0.015$ ). Furthermore,

the ovaries of the *larger* female were very small and poorly developed. From the descriptions of the other animals recorded by Gamble and Taylor it seems that they were also subadults.

In addition to these morphometric differences there were colour differences in some of the small animals. Both females were marked almost exclusively with light brown over the green background; they were strikingly similar to each other yet different from any of the other 130 turtles I examined (see figures 18 and 19, plate 26). There was no apparent uniqueness in the coloration of the subadult male I measured.

Hornell (1927, p. 31) states that the local people believe a resident population dwells in the lagoon at Aldabra, but he seems not to favour this idea. It is interesting to note an observation made in the Galapagos by C. Angermeyer (see Carr 1967, p. 217). She relates that two forms of green turtles exist sympatrically—one, the resident dark form, apparently breeds in the archipelago; the other, a migrant yellow form, apparently does not. Whatever is involved in the movements of these intriguing creatures will become evident only after detailed studies and extensive tagging have been carried out.

Hirth (F.A.O. 1967) tagged five females at Aldabra and two more at Assumption. During the present study only ten nesting females were tagged at Aldabra. Numerous authorities in the western Indian Ocean area have been informed of the tagging programme, and it is planned to continue it.

#### (d) *Breeding biology*

Aldabran females seem to have the same nesting behaviour as females from other localities. Numerous authors (e.g. Carr & Giovannoli 1957; Carr & Ogren 1960; Hendrickson 1958; Moorehouse 1933) have described in detail the stranding, ascent of the beach, wandering on the high beach platform, digging the body pit, digging the nest cup, egg laying, covering the nest, and return to the sea. It seems that these activities are constant throughout the range of the species. Carr & Hirth (1962, p. 18) felt that there were slight differences in the nesting behaviour of Tortuguero and Ascension females, but no quantitative data were presented.

Spurs (1892) and Hornell (1927, p. 39) stated that the Aldabran females laid at least three clutches a year, renesting every 13 to 15 days. My information is consistent with this; and, in fact, this habit of relaying several times a year at approximately two week intervals has been described in all populations of green turtles studied (e.g. Tortuguero—Carr & Giovannoli 1957, p. 8; Carr & Ogren 1960, p. 16; Surinam—Pritchard 1969; p. 93; Guyana—Pritchard 1969, p. 90; Ascension—Carr & Hirth 1962, p. 16; Yemen—Hirth F. A. O. 1967, p. 15; Heron Island—Moorehouse 1933, p. 3; Sarawak—Hendrickson 1958, p. 498).

Spurs (1892) and Hornell (1927, p. 29) estimated the average clutch size at Aldabra at 125 and between 150 and 200 respectively. Both of these estimates are above my own figures (average = 90,  $n = 4$ ) but they are all in the general range of estimates from other localities (table 2).

Hornell (1927, p. 39) estimated between 47 and 50 or more days for 'incubation' (really time for oviposition till emergence from the sand), and my scant information indicates almost 10 weeks. Hornell's figure is more in line with those from other localities (table 2) and was probably from nests at the peak of the breeding season. My period is much longer, probably because it is from a nest at the cooler part of the year. Hendrickson (1958, p. 511) has established that 'incubation' periods vary from one part of the year to the other, depending on environmental conditions.

Egg sizes from Aldabra and other populations are compared in table 2.

Many of the averages in table 2 are drawn from small samples and it will be necessary to increase the sample size in order to get more realistic estimates of the population means. Nevertheless, there is a very clear pattern in this table. Notice that localities are ranked in order of decreasing size for 'adult female straight length'; this ranking is correlated strongly with hatchling straight length and egg diameter rankings. The relation to clutch size is not so straightforward but has the same tendency.

TABLE 2. SUMMARY OF REPRODUCTIVE DATA FROM DIFFERENT LOCALITIES

| locality   | adult female<br>straight length<br>cm | hatchling<br>straight length<br>mm | egg diameter<br>mm | clutch size | 'incubation' period<br>days |         |
|------------|---------------------------------------|------------------------------------|--------------------|-------------|-----------------------------|---------|
|            |                                       |                                    |                    |             | average                     | range   |
| Surinam    | 112.1                                 | 53.5                               | —                  | 142.0       | 58.3                        | (47-64) |
| Ascension  | 108.2                                 | 51.7                               | 54.6               | 115.5       | 59.5                        | (58-62) |
| Guyana     | 106.8                                 | —                                  | 48.0               | ca. 122.0   | —                           | —       |
| Aldabra    | 103.0                                 | 50.1                               | 46.3               | 89.0        | —                           | (47-69) |
| Costa Rica | 100.3                                 | 49.7                               | 45.7               | 110.0       | 55.6                        | (48-70) |
| Ceylon     | 96.0                                  | ca. 51.5                           | 45.5               | —           | —                           | —       |
| Yemen      | 96.0                                  | 46.9                               | 42.4               | 160.0       | 48.0                        | —       |
| Sarawak    | 95.1                                  | —                                  | 40.0               | 104.7       | 55.0                        | (45-80) |
| Heron Is.  | —                                     | 54.0                               | 40.5               | ca. 120.0   | —                           | (65-71) |
| Malaya     | —                                     | —                                  | —                  | 97.0        | —                           | (47-61) |

Data from Balasingam (1965, p. 139; 1967, p. 235) (Malaya); Carr & Hirth (1962, p. 13) (Ascension and Costa Rica); Deraniyagala (1939) (Ceylon); Hirth, F.A.O. (1967, p. 14) (Yemen); Hendrickson (1958, p. 504) (Sarawak); Moorehouse (1933, pp. 4, 7, 10) (Heron Island); Pritchard (1969, pp. 93, 95) (Surinam); Pritchard (1969, p. 90) (Guyana).

It is known that clutch size and size of the female are often strongly correlated in reptiles (Graham 1969; Goin & Goin 1962). Egg size is also correlated in this way and it would follow that hatchling size is likewise correlated.

These measurements are also affected by numerous factors such as season (Hendrickson 1958) and the number of previous clutches (Carr & Hirth 1962, p. 16). When more is known, it may be possible to determine the relationships of these variables more exactly.

#### (e) *Hatchlings*

Table 3 presents mean and standard deviations of various measurements taken from 188 hatchlings from six different clutches. Only one clutch is not from Aldabra; it is from the neighbouring island of Astove. Five clutches were measured in 1968 by me and one in 1964 by R. Honegger.

An analysis of variance on the straight length data from the four large clutches indicates that the inter-clutch variation is significantly greater than the intra-clutch variation ( $p < 0.001$ ); thus, with the present data it is not strictly valid to average together the different clutches in order to obtain a grand average for Aldabra. The bottom row in table 3 should be taken as a preliminary indication only.

The data on straight length of carapace from Aldabra and other localities are presented in figure 2. Unfortunately, these data can only be compared in the light of certain limitations. The problems involved with the Aldabran figures have just been discussed. In other studies, authors have usually not published adequate statistical information with which comparisons



can be made. Also, few authors have been concerned with the problem of intra- and inter-clutch variation *within* a population. Samples of siblings from the same clutch are probably *not* randomly distributed about the population mean and estimates based on averages of such samples will most certainly be biased.

TABLE 3. MEASUREMENTS AND SCALE COUNTS FROM ALDABRAN HATCHLINGS

| date          | locality | no. of speci- mens | carapace              |                      | plastron length<br>mm | head width<br>mm | cara-<br>pace<br>'normal'<br>% | mass/g       |
|---------------|----------|--------------------|-----------------------|----------------------|-----------------------|------------------|--------------------------------|--------------|
|               |          |                    | straight length<br>mm | straight width<br>mm |                       |                  |                                |              |
| 1968          | Astove   | 11                 | 48.45 ± 0.820         | 39.36 ± 0.925        | 41.18 ± 0.751         | —                | 100                            | —            |
|               |          | 2                  | 48.0                  | 38.5                 | 39.0                  | —                | (50)                           | —            |
| 1968          | Aldabra  | 14                 | 47.93 ± 0.829         | 39.14 ± 1.125        | 37.79 ± 0.802         | —                | 78.6                           | 24.21 ± 1.72 |
|               |          | 1                  | 50.0                  | 37.0                 | 39.0                  | —                | (100)                          | 28.0         |
|               |          | 49                 | 51.31 ± 0.862         | 41.57 ± 0.867        | 41.57 ± 0.924         | 16.29 ± 0.924    | 89.8                           | 29.37 ± 0.74 |
| 1964          | Aldabra† | 111                | 50.00 ± 1.388         | 40.6 ± 1.581         | —                     | —                | 86.5                           | —            |
| grand average |          | 188                | 50.07                 | 40.60                | 40.73                 | (16.29)          | —                              | 28.22        |

† Data from R. Honegger (personal communication).

Figures represent average ± one standard deviation.

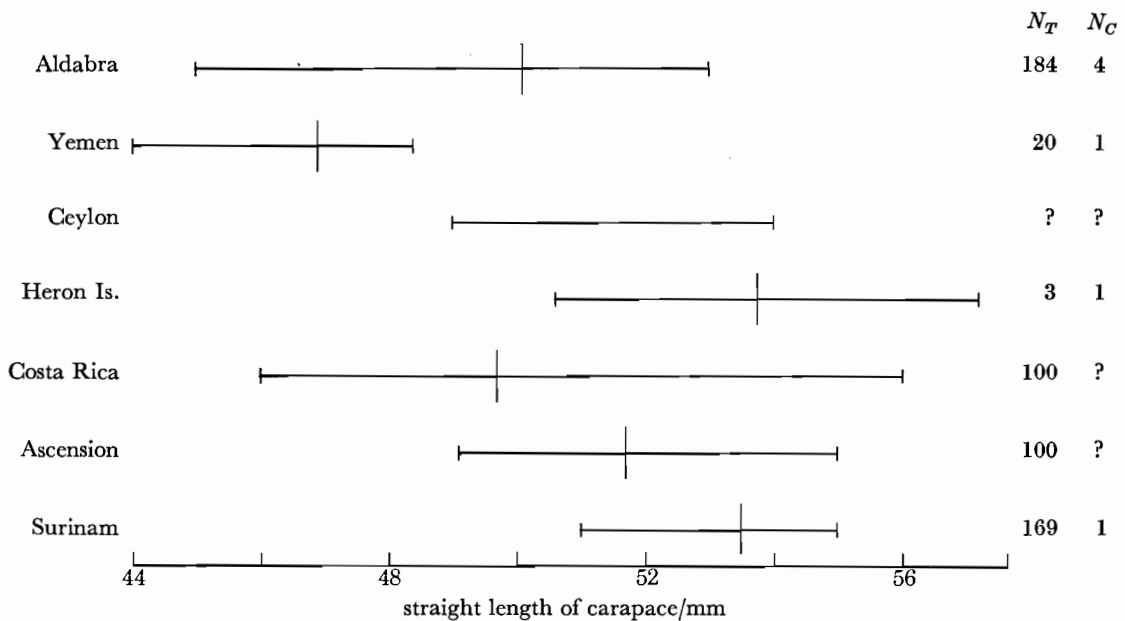


FIGURE 2. Straight carapace length measures from hatchling green turtles. The horizontal line equals the range; the vertical line, the mean (in mm).  $N_T$ , number of turtles measured;  $N_C$ , number of clutches represented. Data from Yemen (F.A.O. 1967, p. 15), Ceylon (Deraniyagala 1939, p. 229), Heron Island (Moorehouse 1933, p. 16), Costa Rica (Carr & Hirth 1962, p. 24), Ascension (Carr & Hirth 1962, p. 24) and Surinam (Pritchard 1969, p. 95).

Even though the samples (figure 2) are small, the amount of overlap in ranges is enough to warrant a certain amount of caution in the interpretation of the figures in table 3. Also, with animals of this size, it is imperative that there be no significant observer bias. Comparisons between Yemen, Costa Rica, and Ascension should not be affected by this, as the same observer (Hirth) has made the measurements from these localities. However, comparisons between, say, Aldabra and Costa Rica may be complicated by such factors; and it is important to devise means of either eliminating or controlling for them.

There is a certain amount of data on other linear measurements on hatchlings from other localities (Carr & Hirth 1962, p. 24; Deraniyagala 1939, p. 238; F. A. O. 1967, p. 15; Moorehouse 1933, p. 16), but these will not be discussed at this time.

(f) *Growth*

There is little information on size change of sea turtles of known age, and what little there is usually deals with captives. It is known that hatchlings do not eat for several days after emerging; Moorehouse (1933, p. 12) found that it took a week before feeding began, while Harrison (1955, p. 638) found animals feeding after  $3\frac{1}{2}$  days. Animals kept on Aldabra began feeding between 3 and 7 days after emergence.

During these first few days the animals are extremely active as Carr (1967) has described. As they are not feeding during this time, the hatchlings must be metabolizing some food store. Moorehouse (1933, pp. 8, 12) found that hatchlings which died several days after emergence were still well endowed with yolk; and Harrison (1955, p. 638) established that hatchlings

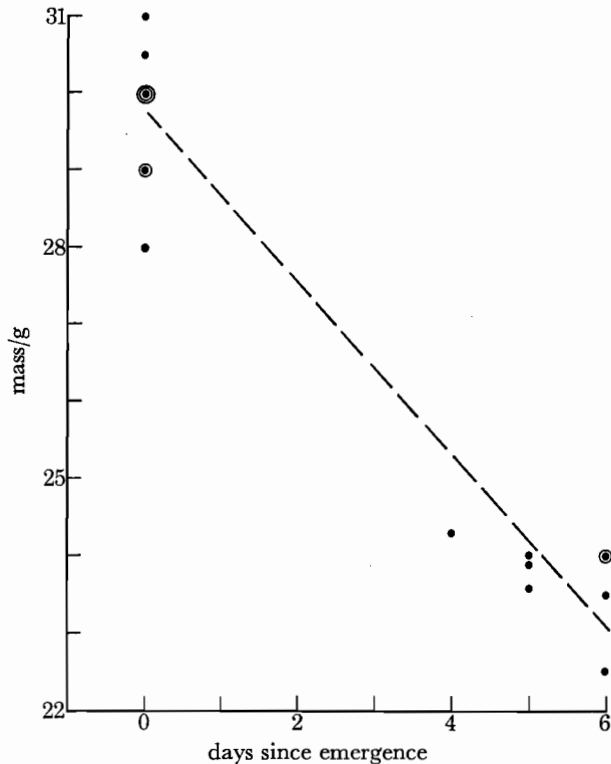
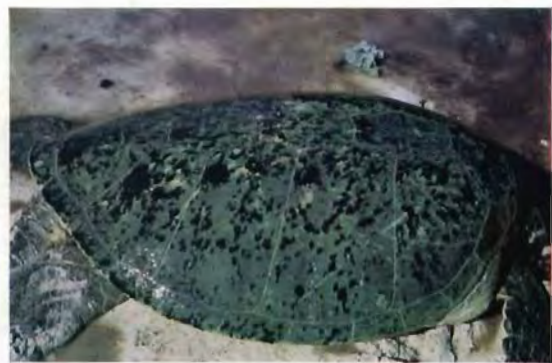


FIGURE 3. Mass loss in eight hatchlings. (The regression line is fitted by eye.)

DESCRIPTION OF PLATE 26

FIGURES 18 to 27. *Chelonia mydas*. 18, subadult ♀ 161: note complete lack of black pigment. 19, subadult ♀ 163: note almost complete lack of black pigment. 20, adult ♂ 229: note almost complete lack of dark pigment. 21, adult ♂ 222: note intensity of dark pigmentation. 22, adult ♂ 156: concentrations of dark pigment in all scales, and many streaks. 23, adult ♂ 66: concentration of dark pigment in only some scales, and almost entirely spotted. 24, adult ♂ 59: no conspicuous concentrations of dark pigment; almost entirely spotted. 25, adult ♂ 247: concentrations in all scales, large spots, but very little dark pigment. 26, adult ♂ 234: very little dark pigment, most of which is brown. 27, adult ♂ 126: conspicuous concentrations of dark pigment, and very little dark pigment elsewhere.





FIGURES 28–35. *Chelonia mydas*. 28, adult ♂ 146: large concentrations of dark pigment and bold streaks. 29, adult ♀ 242: brown pigment *only outside* the concentrated area of dark pigment. 30, adult ♀ 220: brown pigment both inside and outside the concentrated area of dark pigment. 31, adult ♀ 243: predominantly brown pigment with bold streaks. 32, adult ♀ 235: extensive but interrupted areas of dark concentrations. 33, adult ♀ 245: very rich coloration; note the 'bulls-eye' and heavy streaking. 34, adult ♀ 237: very rich coloration; note the 'bulls-eye' and heavy streaking. 35, adult ♂ 49: viewed from behind. Is this what a potential predator sees?

could survive for over a month with no food—apparently living off the yolk. Sixteen animals that died in captivity at Aldabra all had supplies of yolk; these animals were between 0 and 6 days after emergence. In fact, two animals 5 weeks old still had remnants of a yolk sac about 1 cm in diameter.

These animals exhibited a marked decrease in mass as illustrated in figure 3. The average rate of decrease, as represented by the regression line, is 1 g per day. This phenomenon could cause erroneous assumptions if workers compare masses of different hatchlings without keeping the time (after emergence) constant. In fact, this may explain the large differences in the Aldabran data in table 3. The clutch of 14 emerged naturally and were weighed the following morning; the clutch of 49 were removed from the sand after one animal emerged at midday and weighed immediately.

Harrison (1955, p. 638) has indicated that there is a mass gain between the first and second day after emergence (3.5 g). This is somewhat surprising as the hatchlings are *not* eating at that age according to Harrison. In light of Moorehouse's finding—that hatchlings placed in fresh water die very soon (1933, p. 11)—it seems that water may be absorbed or imbibed by the hatchling.

TABLE 4. ANALYSIS OF VARIANCE OF ADULT MEASUREMENTS

st. ln., straight length; st. wd., straight width; p. ln., plastron length; cv. wd., curved width; h. wd., head width.

|                    | sex      |                      |        | season plus<br>sex/season interaction |                |        |
|--------------------|----------|----------------------|--------|---------------------------------------|----------------|--------|
|                    | <i>F</i> | <i>p</i>             | d.f.   | <i>F</i>                              | <i>p</i>       | d.f.   |
| st. ln.            | 55.02    | *** <i>p</i> < 0.001 | 1, 133 | 0.406                                 | —              | 2, 133 |
| cv. wd.<br>st. wd. | 15.00    | *** <i>p</i> < 0.001 | 1, 122 | 0.500                                 | <i>p</i> > 0.2 | 2, 122 |
| st. wd.<br>st. ln. | 0.95     | <i>p</i> > 0.200     | 1, 133 | 1.199                                 | <i>p</i> > 0.2 | 2, 133 |
| p. ln.<br>st. ln.  | 243.44   | *** <i>p</i> < 0.001 | 1, 120 | 0.115                                 | <i>p</i> > 0.2 | 2, 120 |
| h. wd.<br>st. ln.  | 10.004   | ** <i>p</i> < 0.01   | 1, 112 | 1.968                                 | <i>p</i> < 0.2 | 2, 112 |

Data on increase in size of hatchlings have been plotted in figures 4 and 5 along with data from other localities. These data, taken with the *overall* decrease in mass during the initial fasting period, indicate that rate of growth may be sigmoidal as suggested by Carr (in Caldwell 1962*a*, p. 3) and not simply linear as suggested by Hendrickson (1958, p. 519).

There are to date no data to indicate the rate of growth of adult turtles; Carr & Caldwell (1956, pp. 12, 13) and Schmidt (1916) have presented information on rates of growth of wild subadults.

(g) *Adult measurements*

*Sex and season differences at Aldabra*

Histograms of a number of important measurements are shown in figures 6 to 15. Five of these blocks of data was tested with a 2 (sex) by 2 (season) analysis of variance, the results of which appear in table 4. April/May seems the most natural time at which to divide the year into seasons, for this is approximately when the transition from wet season to dry season occurs. This division is also in agreement with that of Hornell (1927, p. 37) who claimed that one population breeds from February to May and another from May to September.

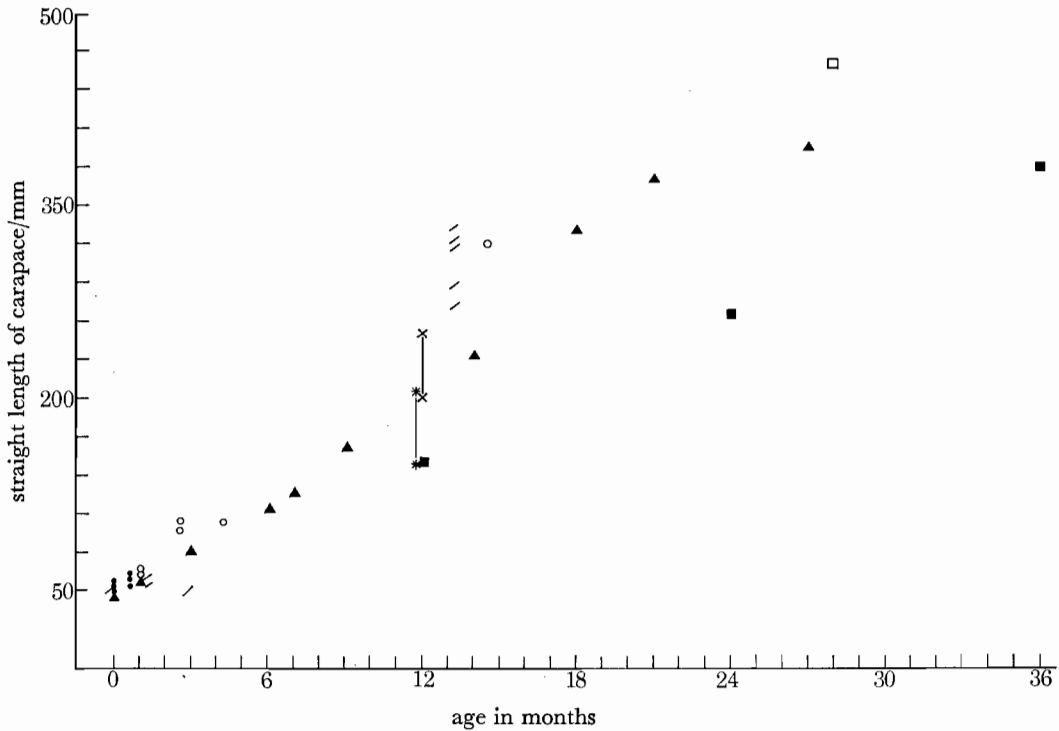


FIGURE 4. Lengths of hatchling and subadult green turtles of known age. \*, Aldabra, 1963/4 (Honegger 1967, p. 11); /, Aldabra, 1968; •, Heron Island (Moorehouse 1933, p. 16); ▲, Sarawak (Hendrickson 1958, p. 518); ○, Ceylon (Deraniyagala 1939, p. 229); ×, East Pacific (Carr 1952, p. 362); □, Assumption (Hornell 1927, p. 24); △, Sarawak (Harrison 1955, pp. 637, 639); ★, Danish West Indies (Schmidt 1916); ■, Costa Rica (Caldwell 1962a, pp. 3, 5). Data on five Aldabran specimens at 13 months from B. Bell (personal communication). Vertical lines for Aldabra and East Pacific represent ranges.

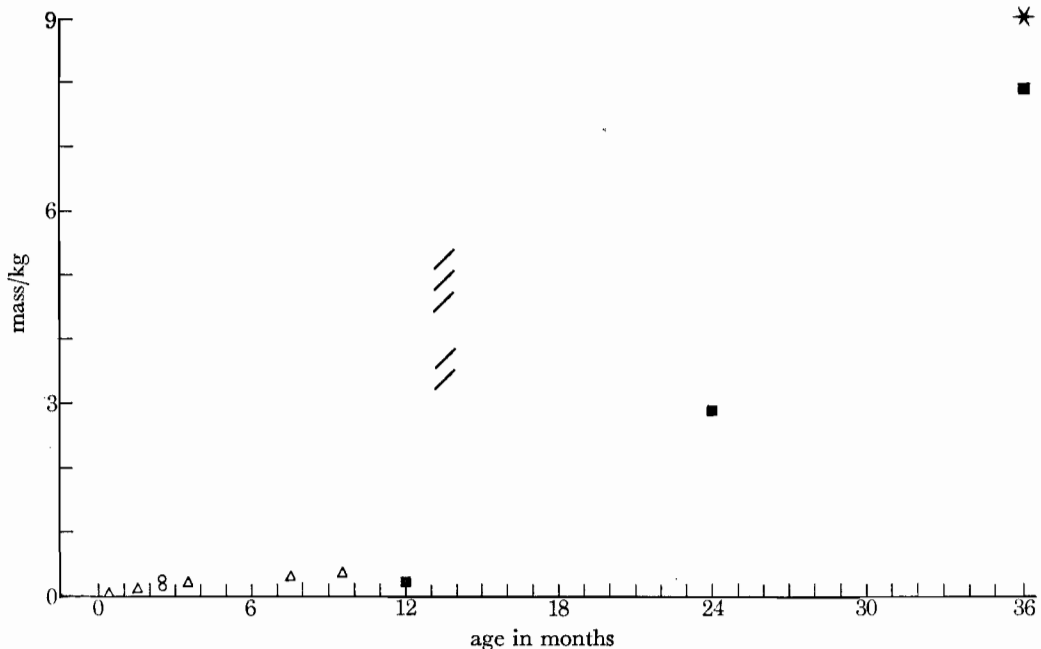


FIGURE 5. Mass of hatchling and subadult turtles of known age. Symbols as in figure 4.

FIGURES 6 TO 15. FREQUENCY HISTOGRAMS OF MEASUREMENTS FROM ADULT ALDABRAN GREEN TURTLES

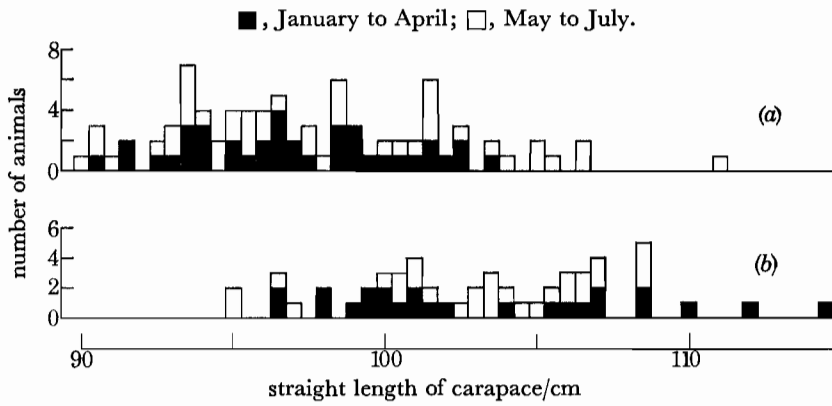


FIGURE 6. Straight length of carapace. (a) Males,  $n = 83$ ; (b) females,  $n = 54$ .

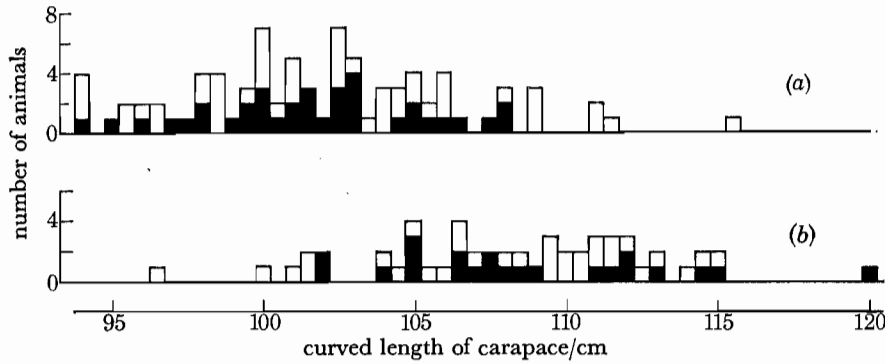


FIGURE 7. Curved length of carapace. (a) Males,  $n = 84$ ; (b) females,  $n = 54$ .

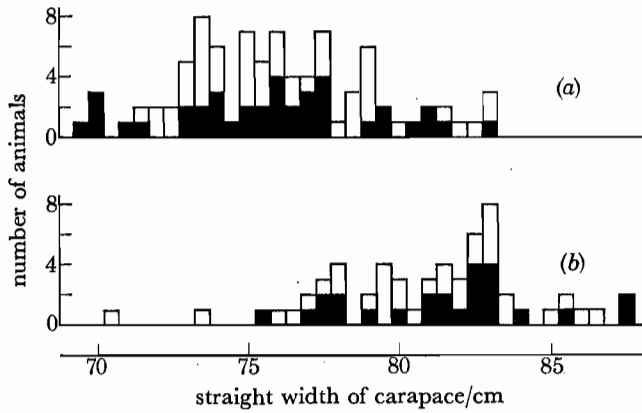


FIGURE 8. Straight width of carapace. (a) Males,  $n = 88$ ; (b) females,  $n = 58$ .

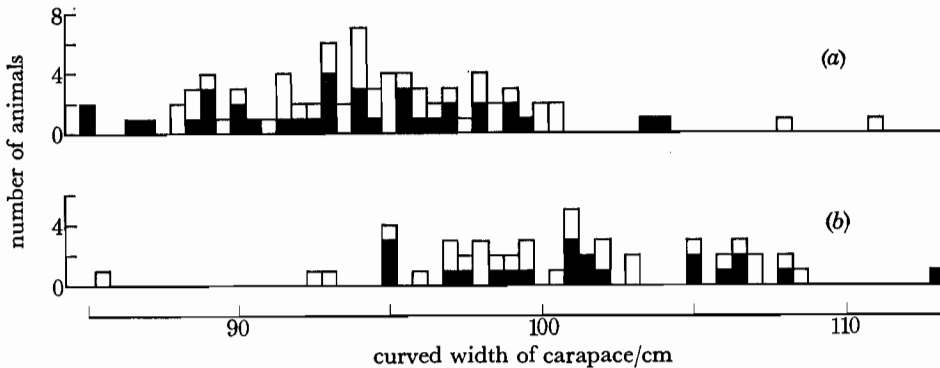


FIGURE 9. Curved width of carapace. (a) Males,  $n = 80$ ; (b) females,  $n = 50$ .

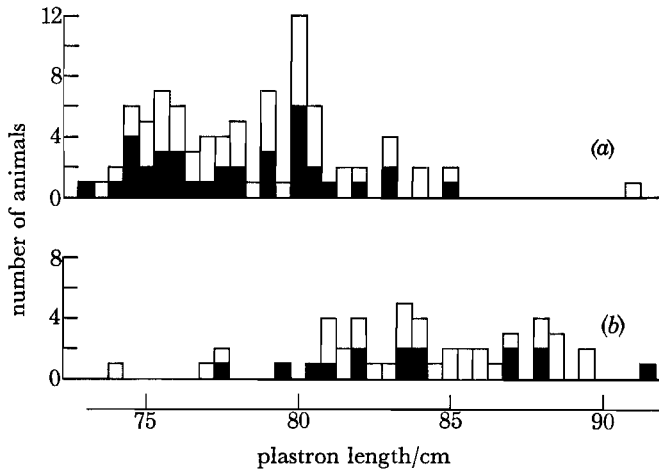


FIGURE 10. Plastron length. (a) Males,  $n = 85$ ; (b) females,  $n = 48$ .

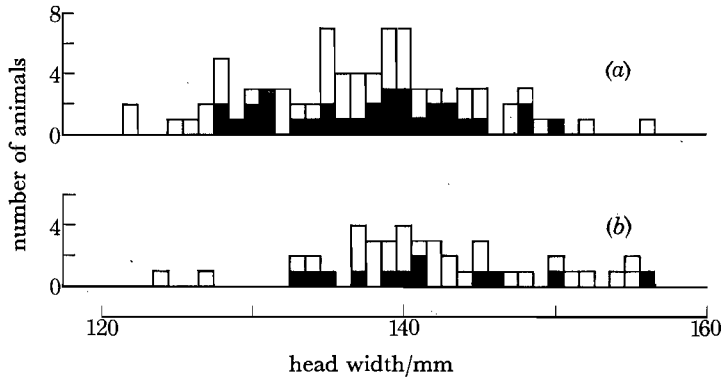


FIGURE 11. Head width. (a) Males,  $n = 81$ ; (b) females,  $n = 45$ .

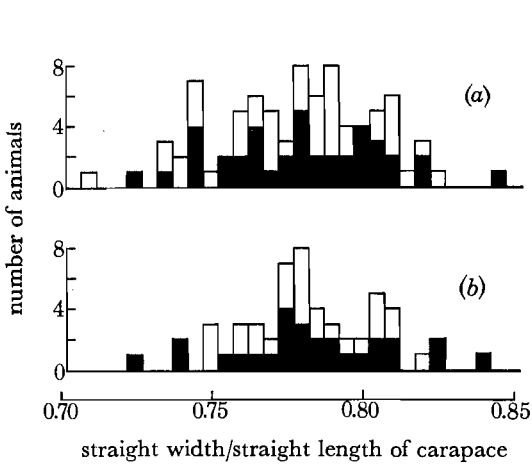


FIGURE 12. The ratio straight width/straight length of carapace. (a) Males,  $n = 83$ ; (b) females,  $n = 54$ .

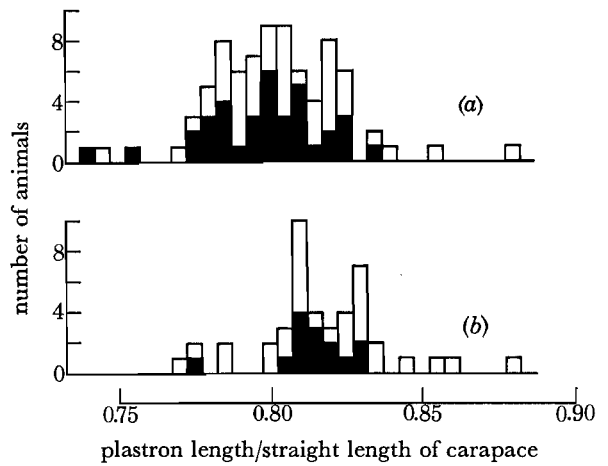


FIGURE 13. The ratio plastron length/straight length of carapace. (a) Males,  $n = 80$ ; (b) females,  $n = 44$ .



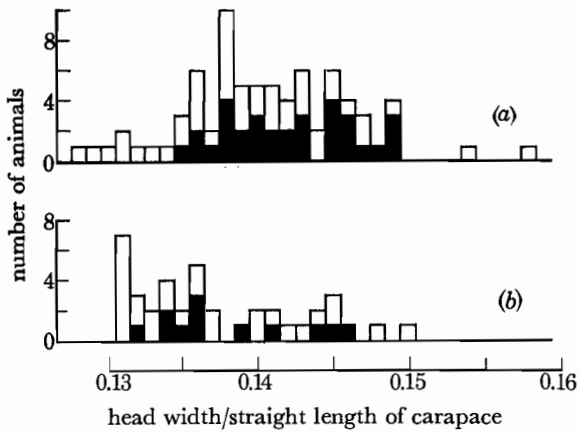


FIGURE 14. The ratio head width/straight length of carapace. (a) Males,  $n = 76$ ; (b) females,  $n = 40$ .

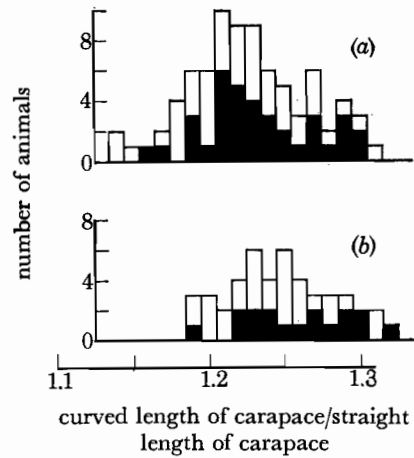


FIGURE 15. The ratio curved length of carapace/straight length of carapace. (a) Males,  $n = 80$ ; (b) females,  $n = 46$ .

There is no indication of any seasonal effect in the histograms or the analysis of variance results; nor is there any effect from a sex-season interaction. On the other hand, sex differences show up very clearly in: curved length, curved width, straight length, straight width, plastron length and head width. The ratios plastron length/straight length, head width/straight length, and straight width/curved width also illustrate sex differences.

Thus, females are on average larger than males and have relatively larger plastrons but relatively smaller heads. Females also have more domed carapaces.

These findings raise a number of problems. First, there are scant data on measurements from *adult* males of any species of sea turtle. Caldwell (1962*b, c*) and Hirth (F. A. O. 1967) deal with measurements of large numbers of male and female green turtles from feeding grounds, but comparisons between sexes are not easy to interpret owing to the inclusion of many different age classes and many subadult animals. Second, accounts in the literature claim that adult males are, on average, larger than females (Carr 1952, p. 348). But these comparisons are based on very small samples (sometimes one animal of each sex).

The fact that Aldabran males are smaller than Aldabran females could be interpreted in two ways. The conventional concept that males are larger than females may be wrong, or there may be something 'abnormal' about the Aldabran population. The latter point seems more likely (although it does *not* necessarily preclude the first). There is good evidence that for the last six years (or more) many more males than females have been removed from the Aldabran populations (see Population, § 3*i*). This would result in a skewed distribution for the males, with very few animals reaching large size because of the decreased chances of survival, which could explain the sex difference in overall size. However, it is necessary to test the conventional view that males are larger than females by measuring populations that are undisturbed by man.

In order to understand more fully the sex differences in body proportions, regression analysis was carried out. These results are presented in table 5. There is a strong *negative* relation between carapace length and the ratio head width/carapace length; this applies to both curved and straight measures. In males this relation is statistically significant; in females it is not, but the same negative tendency still exists. This, together with the fact that females have absolutely larger but relatively smaller heads (figures 11 and 14), indicates that allometric growth is

involved here. Further evidence for allometry is that hatchlings have head width ratios of approximately 0.33 (c.f. table 3), more than twice the value for adults. This simply means that the smaller a turtle the larger is the relative size of its head, and this alone could account for the sex difference in head ratios between the small males and the large females.

TABLE 5. REGRESSION COEFFICIENTS FOR ADULT MEASUREMENTS

| variables |             |            |            |         |
|-----------|-------------|------------|------------|---------|
| dependent | independent | ♂          | ♀          | d.      |
| cv. ln.   | cv. wd.     | 0.737***   | 0.626***   | 1.11    |
| cv. ln.   | st. ln.     | 0.97428*** | 1.0212***  | 0.64    |
| cv. wd.   | st. wd.     | 1.0734***  | 1.4378***  | 1.975!  |
| st. ln.   | st. wd.     | 1.0104***  | 0.95049*** | 0.366   |
|           | p. ln.      | 1.2172***  | 0.98865*** | 1.96!   |
|           | h. wd.      | 4.3253***  | 3.6225***  | 0.68    |
|           | st. wd.     |            |            |         |
|           | st. ln.     | -76.125*** | -48.967    | —       |
|           | p. ln.      |            |            |         |
|           | st. ln.     | -115.58*** | -19.285    | —       |
| cv. ln.   | h. wd.      |            |            |         |
|           | st. ln.     | -276.87**  | -190.15    | —       |
|           | p. ln.      | 1.189***   | 0.9288***  | 10.4!!! |
|           | h. wd.      | 4.1542***  | 4.1581***  | 0.0003  |
|           | cv. wd.     |            |            |         |
|           | cv. ln.     | -33.929*   | -14.09     | —       |
|           | p. ln.      |            |            |         |
| cv. ln.   | -104.61     | -47.69     | —          |         |
| cv. ln.   | h. wd.      |            |            |         |
|           | cv. ln.     | -280.39**  | -204.41    | —       |

\* Regression coefficient is significant at  $p < 0.05$ .

\*\* Regression coefficient is significant at  $p < 0.01$ .

\*\*\* Regression coefficient is significant at  $p < 0.001$ .

! The difference between the regression coefficient for each sex is significant at  $p < 0.05$ .

!!! As above—significant at  $p < 0.001$ .

Abbreviations as in table 4.

The situation with relative length of plastron is quite different. Females not only have absolutely larger plastrons but also *relatively* larger plastrons (figures 10 and 13). In males there is a strong *negative* relation between carapace length and relative plastron length; in females there is a negative relation but it is not significant (table 5). There is also a significant difference between the sexes in the regression of carapace length (either straight or curved) on plastron length (see figure 16). This again shows that females have relatively larger plastrons. Furthermore, hatchlings have larger plastron ratios than males but about the same as females (table 3 and figure 13). Thus, there appears to be an allometric situation in males but *not* in females.

Decrease in rate of plastron growth probably occurs with a complex of secondary sexual characters, most probably closely related with enlargement, both in length and in diameter, of the male's tail. Males may have relatively smaller plastrons for no more reason than to allow for more room in which to accommodate and to manoeuvre the thick muscular tail.

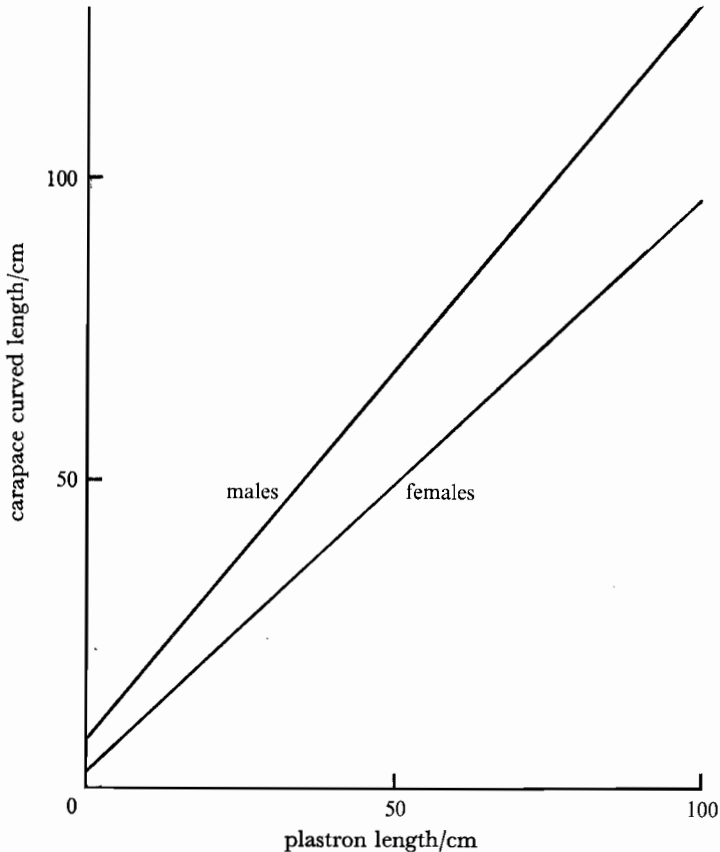


FIGURE 16. Regression of carapace curved length on plastron length. Male line:  $y = 1.189(x) + 8.7959$  cm; female line:  $y = 0.9288(x) + 3.0488$  cm.

There is also a sex difference in the ratio of straight width to curved width as shown in regression lines. The slope of the female line is much greater than the slope of the male line, but for most of the range of measurements it is below the male line. This indicates that females have relatively smaller straight widths, or that females have more domed carapaces. This characteristic has been suggested by Carr (1952, p. 348) but there have been few quantitative data to support it. In many types of chelonians the females are characteristically more domed than the males, which may be a common adaptation to facilitate copulation.

#### *Locality differences*

I have previously mentioned that there are no adequate data on adult males with which the present results can be compared. There are, however, measurements of breeding females from numerous localities. Straight length measures are compared in figure 17. The reasons for these differences are not known; I can see no evidence for any relation between size and latitude, longitude, or island rather than mainland breeding areas. Furthermore, as Carr (1967) has stated, it is not known whether these differences are genetic or environmental.

Comparisons between body proportions (see, for example, Carr & Hirth 1962, p. 22) are difficult to interpret without information on their relation to other variables. Differences could be due to nothing more than allometry (although this might not explain Carr & Hirth's finding)

and differences may be masked by not knowing the correlations or regressions between various measures. Further analysis on these points is still in progress.

As some workers are using straight carapace measures while others are using curved, it is important to know formulae for converting from one set to another. Using the Aldabra data the following relations were derived;

#### Males

$$\text{Curved length} = 0.9743 (\text{straight length}) + 7.006 \text{ cm}$$

$$\text{Curved width} = 1.0734 (\text{straight width}) + 11.562 \text{ cm}$$

#### Females

$$\text{Curved length} = 1.0212 (\text{straight length}) + 3.693 \text{ cm}$$

$$\text{Curved width} = 1.4378 (\text{straight width}) - 15.091 \text{ cm}$$

All the regression coefficients are statistically significant (different from 0).

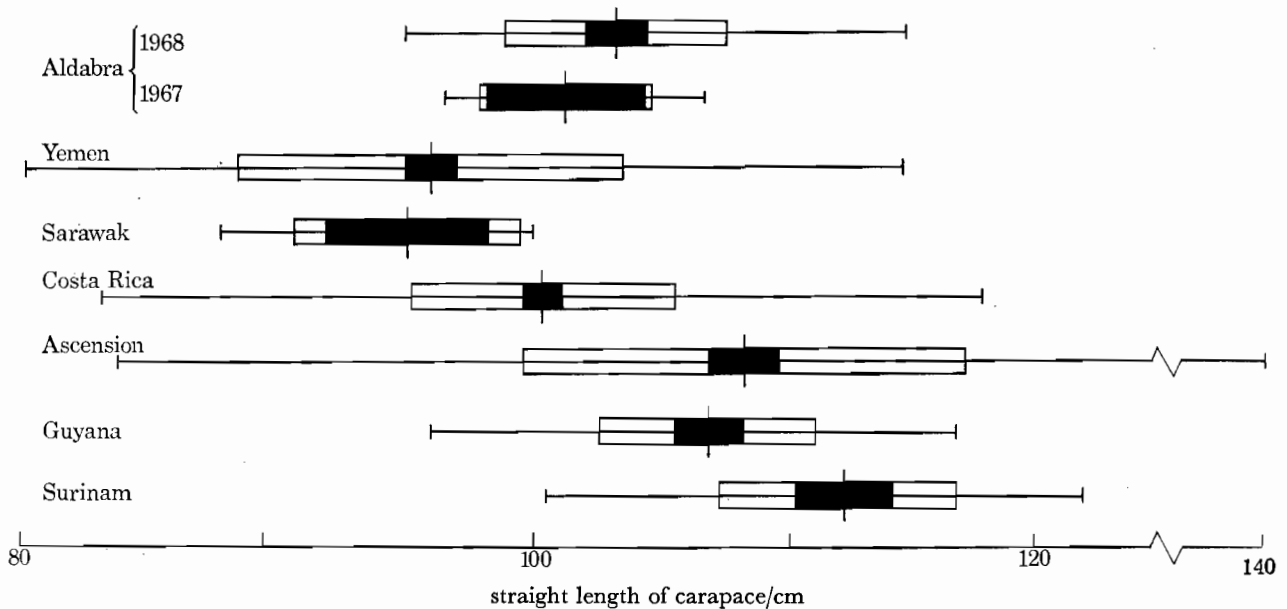


FIGURE 17. Straight carapace length measures for breeding female green turtles. The horizontal line represents range; the open rectangles represent one standard deviation each side of the mean; the black rectangles represent *t* standard errors each side of the mean where  $p = 0.046$ ; the vertical line represents the mean. Data from Aldabra 1967 (Hirth, F.A.O. 1967, p. 32), Yemen (F.A.O. 1967, pp. 5-12), Costa Rica (Carr & Hirth 1962, p. 20), Ascension (Carr & Hirth 1962, p. 20), Sarawak (Hendrickson 1958, p. 519), Guyana (Pritchard 1969, p. 90), Surinam (Pritchard 1969, p. 93).

#### (h) Coloration

Numerous authors have described the general colour pattern of the adult green turtle. Carr (1967, p. 216) discusses subspecific variation in the 'black turtle' and Deraniyagala (1939, p. 229) discusses change in coloration with age; but, on the whole, variations in coloration and their significance have received very little attention.

While measuring the turtles at Aldabra, it became clear that there was a phenomenal amount of colour variation in this population; Hirth (F.A.O. 1967, p. 33), in fact, mentions this in his study. In order to investigate the problem more fully the technique outlined below was used.

Colour photographs were taken with a Miranda 35 mm camera using Kodachrome II film. Usually, two shots were taken for each animal. The developed slides were shuffled and presented in a random serial order with each turtle facing to the right (regardless of which side had been photographed). Five independent observers evaluated five parameters for each slide; these evaluations were based mainly on the condition of the second and third 'right' lateral scutes. The parameters evaluated were: (a) amount of *dark* pigment, expressed as the percentage of the whole area of a scute which was occupied by dark pigment; (b) amount of *black* pigment, expressed as the percentage of the dark pigment occupied by black; (c) amount of *dark brown* pigment, expressed as the percentage of the dark pigment occupied by dark brown; (d) amount of *light brown* expressed as the percentage of the dark pigment occupied by light brown; and (e) the amount of spotting expressed as the percentage of the dark pigment occupied by spots (rather than streaks). Therefore,  $a = b + c + d = 100\%$  of the dark pigmented area—but *not* 100% of the total scute area. For each animal and each parameter an average was taken.

TABLE 6. MEANS AND STANDARD DEVIATIONS OF VARIOUS COLOUR PARAMETERS FOR MALE GREEN TURTLES

| parameter                  | males         |
|----------------------------|---------------|
| amount dark pigment        | 48.85 ± 23.87 |
| amount black pigment       | 74.93 ± 16.84 |
| amount dark brown pigment  | 14.75 ± 13.42 |
| amount light brown pigment | 9.61 ± 9.10   |
| amount spots               | 79.68 ± 25.31 |
| degree of concentration    | 2.25 ± 0.84   |
| placement of brown         | 1.00 ± 1.07   |

Two discrete variables were also evaluated. The first, degree of pigment concentration was rated as: 1, *no* scute with concentrations; 2, *some* scutes with concentrations, or 3, *all* scutes with concentrations. (A 'concentration' is a conspicuous large area of dark pigment in the posterior-medial corner of the scute.) The second discrete variable, placement of brown pigment in relation to the concentrations, was rated as either: 0, not applicable to this animal (because it has no concentrations or no brown pigment); 1, brown pigment found *only outside* the concentration; 2, brown pigment found *only inside* the concentration; or 3, brown pigment found *both* inside and outside the concentration. One hundred and thirty-two slides were analysed in this way (see figures 20 to 35, plates 26 and 27).

The general tendency is for females to be richly pigmented with browns. In most cases, brown forms a 'bullseye' effect by being conspicuously inside the area of concentrated dark pigment. Females are also more streaked than spotted. Males, on the contrary, are more spotted; very few have brown inside the area of dark pigment concentration and there is much less tendency to have rich pigmentation with brown. In fact, males are often not very pigmented at all. Table 6 summarizes these data for males; note the large amount of variation.

In order to define the colour-sex relation more clearly, discriminant analysis was carried out. Many combinations of the colour variables were used in an attempt to get a good prediction of sex by means of the colour data; the most important variables were found to be amount of spotting and the placement of brown in relation to the concentration of dark pigment. The predictive formula for sex using these two variables is:

$$-0.003858 (\text{percentage spotting}) + 0.057551 (\text{value for placement of brown})^2 + 1.3794 = X.$$

If  $X$  is less than 1.5 the animal is a male; if more than 1.5, the animal is a female. This will predict correctly about 85 % of the animals. Although this is far from a perfect prediction, it is at least a reasonable beginning. It is hoped to be able to tie in sex differences with measurements in order to increase the accuracy of the prediction; this work is still in progress.

The reader may wish to compare photographs of the Aldabran animals published here with photographs of animals from other localities. These can be found by consulting the references listed in table 7.

TABLE 7. PHOTOGRAPHS OF GREEN TURTLES ILLUSTRATING SEXUAL DIFFERENCE IN COLORATION

Of the animals listed here only one female (plate 26 in Carr 1967) does not fit the stereotyped condition for its sex. Some Costa Rican animals may be represented twice.

| locality        | male description                | female description                                                                     | reference                                 |
|-----------------|---------------------------------|----------------------------------------------------------------------------------------|-------------------------------------------|
| Baja California | spotted, no concentrations      | with concentrations and streaked                                                       | Carr 1952, p. 358                         |
| Costa Rica      | no dark pigment                 | streaked, many shades of dark pigment                                                  | Carr & Ogren 1960, plates 2, 5, 6, 7      |
| Costa Rica      | —                               | rich, brown inside, streaked, spotted                                                  | Carr 1967, plate 6<br>Carr 1967, plate 26 |
| Costa Rica      | spotted and little dark pigment | streaked and many shades of dark pigment                                               | Carr 1967, plate 16                       |
| Sarawak         | —                               | ?                                                                                      | Hendrickson 1958, plates 4a etc.          |
| Sarawak         | —                               | ? streaked                                                                             | Harrison 1955, plate 24                   |
| Yemen           | spotted, no concentrations      | with concentrations, streaked                                                          | Hirth, F.A.O. 1967, pp. 47, 48            |
| Costa Rica      | —                               | streaked, many shades of dark pigment, with concentrations<br>? brown inside, streaked | Parsons 1962, plates 107 and 108          |

The material summarized in this table is adequate for only the most preliminary statement. It appears as if sexual difference in coloration of green turtles is a common phenomenon over their entire range. This has important practical applications, for it is now possible to estimate the sex of subadult specimens whose conventional secondary sexual characters are not yet developed. But it will be necessary to compare the present results with data from other localities. Hopefully, workers in the future will take note of colour patterns—ideally taking coloured photographs *with* colour keys. It would also be a great aid if such photographs were deposited in national museums; this will be done with the present photographs when funds are available.

Beyond the practical applications is the problem of why there should be a sexual difference in coloration. Two causes are likely. A 'characteristic' colour pattern in the female could be an important sign stimulus in courtship, but next to nothing is known about this aspect of turtle biology. If the pattern of coloration is regarded as either disruptive or cryptic (which seems reasonable), then it may be that males and females are exposed to different selective pressures such as predators. Perhaps the different sexes live in different habitats or against different backgrounds.

There is also the problem of the immense variability in coloration. Again, this may be a response to predation, for diversity in coloration would decrease the hunting efficiency of a visual predator (Croze 1967; Sheppard 1958, p. 147).

*(i) Population size and structure*

Previous evidence that males are much smaller than females (Adult measurements §3g) indicates that hunting pressures are not equal on both sexes, but that more males than females are taken. This is further substantiated by examining catch data. In 1963/4 Honegger (1967) found only males captured at Aldabra; in 1964, 1965, and 1966 far more males than females were sent from the outlying islands (Aldabra, etc.) to Mahé (Hirth, F. A. O. 1967, p. 36); Hirth also (p. 33) found only males at the Aldabra kraal in 1967, and I witnessed a very large preponderance of males taken in 1968 (about 2:1). If there were no differential predation then the chances of such an occurrence (more males than females for 6 years) would be very small ( $p = 0.016$ , sign test); thus, I must assume that equal numbers of males and females are *not* usually taken, at least in recent years.

The reasons for this preponderance of males in the catch are probably very simple. A great number of turtles are harpooned, and most are taken while mating because turtles are relatively stationary and very vulnerable during copulation. If many males court a female or stay around a copulating pair (see Mating, §3b), then more males will be vulnerable to the harpoon. The turtlemen claim that they can pick off courting or accessory males one by one until only the female or the copulating pair is left. Furthermore, males are more vulnerable during copulation because they are on top, physically shielding the female. Thus, the chances of harpooning a male must be far greater than of harpooning a female.

In the past century and the earlier part of the present, authors noted that, on the whole, far more females than males were captured (e.g. Hornell 1927, p. 32). This was due to the great numbers of nesting females turned on the beaches. Because of protective legislation—but more probably because of the greatly diminished populations—few nesting females are now captured. This may be evidence for a drastic change in population structure, but direct evidence is still required to support statements such as made by Hirth (F.A.O. 1967, p. 36): ‘There is no doubt that males greatly outnumber females around Aldabra and Assumption . . .’

Information relating to population size is scant, but it is clear that the present populations of green turtles at the Aldabras are vastly diminished from their condition last century. In 1892, Spurs predicted that he would secure 12 000 animals at Aldabra. Hornell (1927, p. 27) describes how between 200 and 300 turtles used to be turned in a night at Assumption. There are nothing like these numbers at Aldabra now; the annual catch, with high intensity hunting, is only a few hundred.

This is ample evidence for the pessimistic predictions expressed by naturalists who discuss the decline of Aldabran turtles. However, making population estimates is yet another problem. Two population estimates for the green turtles at Aldabra have appeared in the literature. Gaymer (1966) ‘guessed’ that the population was roughly 6000; his assumptions are, however, open to considerable doubt. Hirth (F. A. O. 1967, p. 35) ‘believes that now there are less than 1000 female green turtles nesting on Aldabra each year’, there is *no* indication of how this figure was arrived at. I do not have enough data to make a very meaningful estimate, but feel that Hirth’s figure is of the right order of magnitude (cf. the grand total of nests and ‘pits’ in table 1 = 405). It will be necessary to collect data systematically from a number of beaches in order to arrive at a meaningful estimate of the female population; the male population will be more difficult to estimate accurately.

*(j) Predation*

A variety of animals have been accused of preying on hatchlings and the eggs of Aldabran green turtles (Hornell 1927, p. 40; Honegger 1967). Veevers-Carter (1962) even claimed that flamingoes (*Phoenicopterus* sp.) ate hatchlings. Unfortunately, data relevant to predation are very scarce. The only definite cases of predation on hatchlings that I observed involved ghost crabs (*Ocyropode* sp.) catching hatchlings as they went down to the sea. Ghost crabs were also found burrowed into nests. There was no indication whatsoever that hermit crabs (*Coenobita* sp.), coconut crabs (*Birgus*), feral cats, pied crows, sacred ibises, or any other creature (other than turtles themselves) dug into nests—although these potential predators were common on the nesting beaches.

A number of aquatic predators have been suggested by various authors; by far the most common is the shark (Spurs 1892; Voeltzkow 1897; Honegger 1967; Hornell 1927; Travis 1959). Voeltzkow mentions the finding of a turtle in a shark's stomach, and the other authors call attention to large wounds that are found on the Aldabran turtles. Recent information confirms this situation. Gamble reported a small (subadult) turtle in the stomach of a large tiger shark (*Galeocerdo*) caught 2 August 1968. Of 155 adult turtles examined, the following abnormalities were found; large piece of carapace missing—three animals (2%); small piece of carapace missing—eleven animals (7%); and large piece of flipper missing—seven animals (5%). There is no proof that these animals had been attacked by sharks, but some of them had clearly been attacked by something large (unless they were very small when attacked).

*(k) Symbionts*

Information on turtle symbionts is limited; Hendrickson (1958, p. 52) gives a detailed account of symbionts of Sarawak turtles. In other localities authors have claimed that green turtles are not often infested—at least with barnacles (Carr, Hirth & Ogren 1966, p. 4; Hirth, F. A. O. 1967). At Aldabra, the situation seems to be very different for about 88% of the 65 turtles examined had barnacle infestations, some had as many as 230 barnacles on them. Two species of barnacle have been identified by W. Smith: *Chelombia testudinaria* and *Platylepas hexastylus*. Although Hendrickson (1958, p. 524) reported burrowing barnacles in the Sarawak turtles there is no evidence of them in the Aldabran green turtles (see Loggerhead §5). Detailed analysis of the barnacle data is still in progress.

Leeches were found on several turtles caught fresh from the sea. Isopods were found on one animal. Mosquitoes and horseflies were found on turtles above water; these have been identified by B. H. Cogan as *Aedes fryeri* and *Neavella albipectus* respectively. Four turtles were examined internally and only one specimen of an internal parasite was found; *Diaschistorchis* sp., identified by C. A. Wright.

*(l) Feeding*

Although there have been few studies of feeding in green turtles, most authors are in agreement that this species is mainly herbivorous. Table 8 summarizes information on genera of plants eaten; it is notable that very few details have been published.

In the present study six samples of stomach contents were collected from four adult males and two subadult females. These samples were analysed by J. D. Taylor and the results are presented in table 9. *Cymodocea* is not only the most common genus by occurrence but also by volume. The rare occurrence of *Thalassia* is somewhat surprising in the light of findings from



other studies (cf. table 8); its failure to appear as an important food item may be due to the small sample of stomachs taken. Although *Gelidium* and *Laurencia* are respectively second and third in frequency of occurrence, it is probable that they are *not* taken selectively; Taylor has suggested that they are taken incidentally simply because they grow in close association with *Cymodocea*. *Caulerpa*, however, seems to have been selectively taken, for it was the dominant genus in a food sample. None of the last four genera reported in table 9 (*Gelidium*, *Laurencia*, *Caulerpa* and *Codium*) has been recorded as having been eaten by *Chelonia*, and it is not known how important they are as food items.

TABLE 8. GENERA OF FOOD PLANTS RECORDED FOR *CHELONIA MYDAS*

| locality           | <i>Fucus</i> | <i>Sargasso</i> | <i>Zosteria</i> | <i>Cymodocea</i> | <i>Thalassia</i> | <i>Halophila</i> | <i>Enhalus</i> | <i>Posidonia</i> | <i>Halodule</i> | <i>Gelidium</i> | <i>Laurencia</i> | <i>Codium</i> | <i>Caulerpa</i> | <i>Sagittaria</i> | <i>Valisneria</i> | source                     | details presented | number of specimens |
|--------------------|--------------|-----------------|-----------------|------------------|------------------|------------------|----------------|------------------|-----------------|-----------------|------------------|---------------|-----------------|-------------------|-------------------|----------------------------|-------------------|---------------------|
| West Indian Ocean  | .            | a.              | .               | ay.              | .                | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Hornell 1927, p. 40        | .                 | .                   |
|                    | .            | .               | .               | ay.              | .                | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Veevers-Carter 1962, p. 3  | .                 | .                   |
|                    | .            | .               | .               | a.               | a.               | .                | .              | .                | .               | a.              | a.               | a.            | a.              | .                 | .                 | this paper                 | +                 | 6                   |
| Gulf of Aden       | .            | .               | .               | .                | .                | .                | .              | a.               | a.              | .               | .                | .             | .               | .                 | .                 | Hirth, F.A.O. 1967, p. 17  | +                 | > 100               |
| East Indian Ocean  | .            | .               | x.              | x.               | x.               | x.               | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Deraniyagala 1939, p. 234  | .                 | .                   |
| East Pacific Ocean | a.           | a.              | .               | .                | .                | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Carr 1952, p. 361          | +                 | 10                  |
| Atlantic Ocean     | .            | .               | .               | .                | x.               | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Carr & Ogren 1960, p. 11   | .                 | .                   |
|                    | .            | .               | x.              | .                | x.               | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Carr 1952, p. 353          | .                 | .                   |
| Florida            | .            | .               | .               | .                | .                | .                | .              | .                | .               | .               | .                | .             | .               | ?                 | ?                 | Carr 1952, p. 353          | .                 | .                   |
| Gulf of Mexico     | .            | .               | .               | sa.              | sa.              | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Carr & Caldwell 1956, p. 2 | .                 | .                   |
| general            | .            | .               | x.              | .                | x.               | .                | .              | .                | .               | .               | .                | .             | .               | .                 | .                 | Pritchard 1967, p. 200     | .                 | .                   |
|                    | .            | .               | x.              | .                | x.               | .                | x.             | .                | .               | .               | .                | .             | .               | .                 | .                 | Parsons 1962, p. 2         | .                 | .                   |

a., adult; sa., subadult; y., young (hatchling); x., age not designated.

TABLE 9. STOMACH CONTENTS OF SIX GREEN TURTLES AT ALDABRA

| specimen number    | sex | straight length cm | <i>Cymodocea</i> | <i>Thalassia</i> | <i>Gelidium</i> | <i>Laurencia</i> | <i>Caulerpa</i> | ' <i>Codium</i> ' | undetermined algae |
|--------------------|-----|--------------------|------------------|------------------|-----------------|------------------|-----------------|-------------------|--------------------|
| 109                | ♂   | 98.5               | x                | .                | x               | .                | .               | x                 | .                  |
| 110                | ♂   | 96.5               | xxxx             | .                | .               | .                | .               | .                 | .                  |
| 111                | ♂   | 96.5               | xxx              | x                | .               | .                | .               | .                 | .                  |
| 162                | ♂   | 101.5              | .                | .                | .               | .                | xxx             | .                 | x                  |
| 161                | ♀   | 87.0               | xxx              | .                | x               | x                | .               | .                 | .                  |
| 163                | ♀   | 84.5               | x                | .                | x               | x                | .               | .                 | .                  |
| number of stomachs |     |                    | 5                | 1                | 3               | 2                | 1               | 1                 | 1                  |

xxxx, only genus present; xxx, dominant genus present; x, genus present.

Several authors (e.g. Wheeler 1953, p. 144) have claimed that the marine pastures which occur at Aldabra are insufficient to feed the hordes of turtles that (used to) occur there; Carr & Ogren (1960, p. 11) have suggested a similar situation for Ascension Island. In both cases this lack of adequate food is used as evidence for migrations from breeding grounds to feeding grounds; but there are as yet few studies of biomass of food available to turtles or their food requirements.

Randall (1965) has examined the sea grasses in the West Indies and estimated that they could support a very large population of green turtles, but he gives no figures. Hirth (F. A. O. 1967, p. 17) has made some interesting finds on the feeding pastures in the Gulf of Aden. He estimates that removal of 1.7 m<sup>2</sup> of prime *Posidonia* (above ground level) would yield roughly 2.3 kg (5 lb) of wet plant materials—approximately the mass of the stomach contents of a well-fed turtle. Deraniyagala (1939, p. 234) stated: 'Under natural conditions this turtle grazes in its algal

pastures almost as continuously as an ordinary ruminant, and digestion is apparently as rapid, but upon removal from water this process is retarded and specimens slaughtered four days after capture contained comparatively fresh remains of their last meal. Other turtles placed in sea water shortly after capture evacuated every few hours and when slaughtered after about twelve hours, their stomachs were empty'.

Thus, with the information presently available one could estimate the daily requirements of an adult, breeding green turtle at 4.5 kg (10 lb) of wet plant material (see appendix I).

In order to evaluate the biomass of food plants available in Aldabra I have estimated the areas of bottom types surveyed by Taylor (in preparation). His map indicates the following areas:

*Cymodocea/Thalassia* meadows inside the lagoon—11.875 km<sup>2</sup>

'Dense algae' (*Caulerpa*, *Hydroclathrus*, *Halimeda* and *Chaetomorpha*)—6.593 km<sup>2</sup>

Reef platform (*Cymodocea* and *Halodule*—not entirely prime habitat)—20.593 km<sup>2</sup>.

Also, there are some 82.5 km<sup>2</sup> of 'sparse algae' in the lagoon but as this includes such species as *Halimeda* (a calcareous green alga) and no prime habitat I have not included it in the estimation of available food. By the calculations described in appendix I it seems that the standing crop of marine plants at Aldabra could support about 183 000 migrant turtles.

If, on the other hand, the turtles were not migratory but permanent residents, the standing crop would support about 30 000 adult animals; and if individuals bred triennially (see Carr 1967; Harrisson 1955; Hendrickson 1958), then about 10 000 resident animals would breed a year. Thus, the difference between potential numbers of breeding animals in migratory and non-migratory populations is a factor of nearly 18. It is probable that in the past this was an important factor involved in the migrations of animals breeding at Aldabra. However, it is highly unlikely with the decimated populations of present, that this factor is of much importance.

It must be emphasized that these estimates are based on many assumptions. The *Thalassia* biomass per area data are from Florida; the estimates for productivity of 'dense algae' and reef platform are very rough; data on mass of stomach contents are from non-breeding animals in the Gulf of Aden eating *Posidonia*; figures for rate of digestion and daily requirements are very approximate; average length of stay at Aldabra is known for neither males nor females. Nevertheless, these estimates portray an order of magnitude and illustrate the effect of migration on the number of animals that could breed at Aldabra. It will be necessary to test the applicability of these assumptions for Aldabra and to obtain a more direct estimate of the biomass available.

#### (m) Orientation

Pilot tests with both hatchlings and adult females gave results consistent with the findings of Ehrenfeld & Carr (1967) and Ehrenfeld (1968). Both hatchlings and adult females moved directly from the beach crest to the sea *except* when the seaward horizon was darkened by heavy rain storms. One adult female, on finishing her nesting activities at daybreak, wandered inland towards the brightest part of the horizon; at this time the seaward horizon was literally black with a huge rain storm. When the storm had finally cleared, the female, which had wandered nearly 50 m inland up the face of a dune, quickly reoriented toward the sea. Another female who had finished nesting became disoriented by a storm and was moving out across a very treacherous stretch of terrain. I drove her back to the pocket beach from which she had emerged and headed her into the wave-washed sand. However, she persisted in heading *inland* toward the brightest part of the sky. Finally, she was actually driven into the sea.

Results of orientation tests with hatchlings are shown in figure 42. In only three out of 20 trials was the correct seaward heading taken from the start; in the other 17 trials the hatchlings apparently were disoriented because of a very large dark storm front over the seaward horizon. Their degree of disorientation is clearly illustrated by: moving inland when placed on

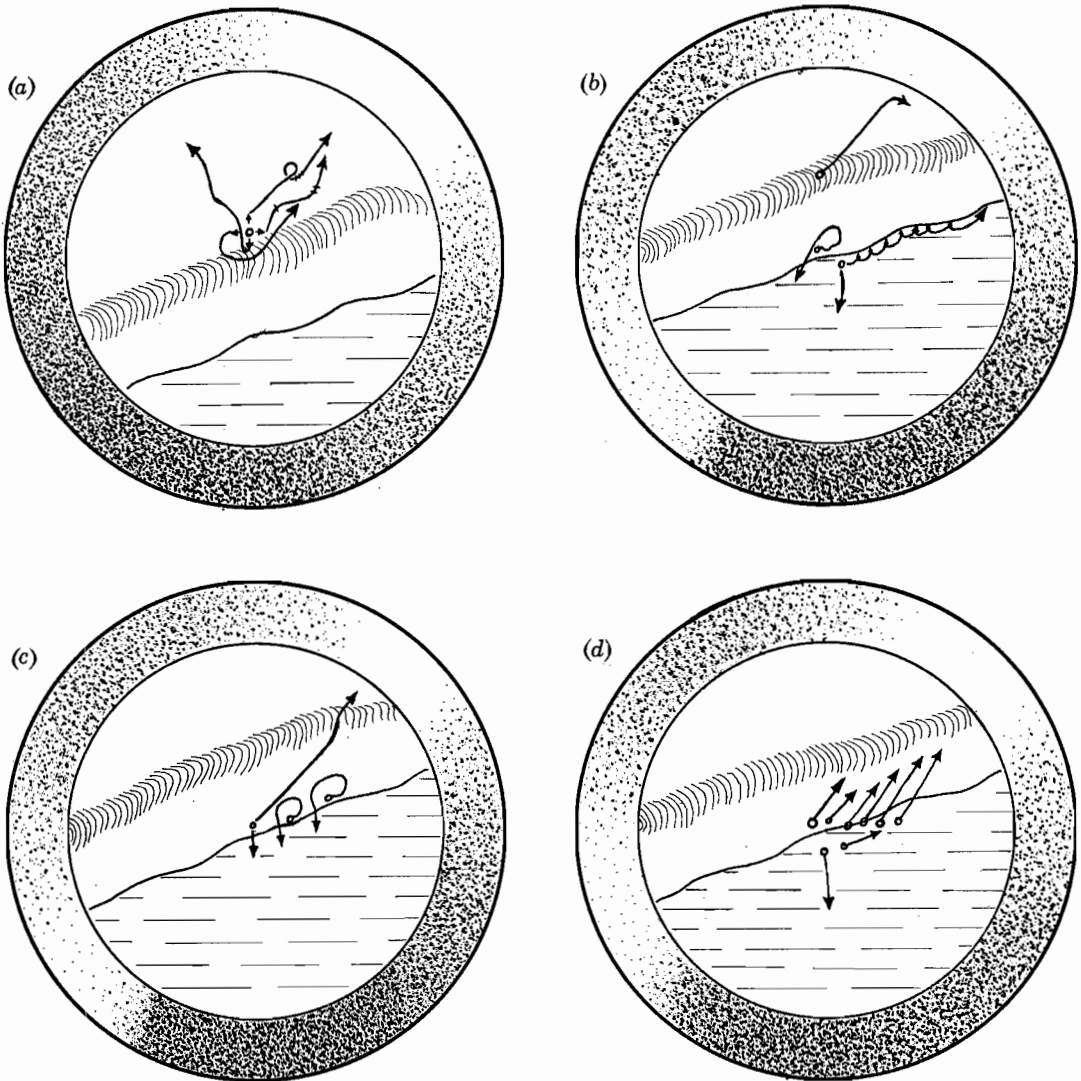


FIGURE 42. Orientation of hatchling turtles during a storm at sea.  $\circ$ , Point of release;  $\rightarrow$ , track taken;  $\dashrightarrow$ , track with long, deliberate pauses. The succession of short curved lines is the beach crest; the wavy line and dashed area at the bottom right of each picture is the ocean. The density of stipling in external circle indicates relative amount of light on horizon. (a) 07h00 5 February: four animals released individually; (b) 17h30 5 February: three animals released individually—one tested twice; (c) 17h45 5 February: four animals; (d) 14h30 6 February: two animals tested six times each and individually.

the beach crest—regardless of initial heading (figure 42a); moving inland when placed on the beach crest, and attempting to come ashore numerous times even though placed in the water (figure 42b); moving up the beach away from the sea when placed less than 2 m from the water, and initially failing to orient properly and requiring several minutes to orient to sea, even though placed at the edge of the water (figure 42c); taking an inland heading when placed

2 m from the water, on wave-washed sand, and actually in the water (figure 42*d*). These results strongly indicate the importance of visual cues.

Carr (1967, pp. 84, 85) has suggested that there are other important cues involved in seaward orientation such as sight of the sea or its white breakers, texture and gradient of the substratum and moisture of the substratum. In essence, he postulates a sort of summation effect in which the responses to these additional stimuli combine to form a stronger response. Unfortunately, my data are not detailed enough to be able to confirm this. It is clear, however, that whatever additional stimuli may be operative, brightness of the horizon is a very important one.

Orientation of hatchlings in the sea is not at all understood; it has been suggested that there may be a switch from visual orientation to some other types of orientation on entering the sea (Carr 1965, p. 82). The movements of hatchlings as they crossed the reef platform at Aldabra indicated that they were still orienting toward bright horizons. One animal continued to bump into bright, alga-covered rocks as it made its way to the open ocean; its persistent bumping into rocks was not accidental, for it would alter its course consistently from one rock to another as it swam out.

The longevity of the visual response was illustrated off Astove, where one night a light was hung over the side of the ship. Over a dozen hatchlings homed in on this light, apparently *en route* from the beach to the open sea. Carr & Hirth (1962, p. 27) mention a similar occurrence. There was no indication that hatchlings have a standard response to currents, for they would swim with, against, or across currents in no predictable manner as they made their way across the reef platform.

#### 4. HAWKSBILL *ERETMOCHELYS IMBRICATA* L.

The hawksbills at Aldabra are known for their 'blonde' shell which is said to be in greater demand than most other types of 'tortoiseshell' (Hornell 1927, p. 10); however, very little quantitative data on these animals exists.

##### (a) Occurrence

The Seychellois turtlemen claim that hawksbills are very common at Passe Houareau and Main Channel, and records of sightings confirm this. Hawksbills have been sighted at Passe Houareau (six times inside the lagoon); Main Channel (outside the lagoon); Passe du Bois; NE Lagoon; NW Lagoon; west Lagoon; and SE Lagoon in 2.5 m of water (figure 1). It is notable that most sightings of this species at the surface were in the lagoon. Aqualung divers recorded them at depths of 80 m (J. N. Lythgoe, personal communication). Sightings have been made round the year, but most are from the dry season.

##### (b) Measurements

TABLE 10. MEASUREMENTS OF 5 HAWKSBILLS

| specimen no. ...            | 1    | †2   | †3   | †4   | 5    |
|-----------------------------|------|------|------|------|------|
| sex ...                     | F    | F?   | F?   | F?   | F?   |
| parameter                   |      |      |      |      |      |
| carapace length straight/cm | 61.5 | 38.0 | 39.0 | 36.0 | 73.0 |
| carapace length curved/cm   | 65.0 | 39.5 | 40.0 | 37.5 | 78.0 |
| carapace width straight/cm  | 47.5 | 30.0 | 31.0 | 29.5 | 55.5 |
| carapace width curved/cm    | 56.5 | 34.0 | 35.0 | 33.5 | 65.0 |
| plastron length/cm          | 47.5 | 29.0 | 27.5 | 26.5 | 54.5 |
| head width/cm               | 9.1  | 5.4  | 5.4  | 5.1  | —    |

† Data from J. Gamble & R. Hughes (personal communication).

*(c) Scallation*

All five specimens had 11 marginals and three postoculars on each side. The following observations are based on specimen 1 (see figures 37 and 38, plate 28):

- (1) Medial keel only on last four centrals.
- (2) Only last central with lateral ridges that converge posteriorly.
- (3) Laterals without ridges running from the posterior point of each lamina.
- (4) Plastron keels not prominent.
- (5) Margin of carapace serrate.
- (6) Carapace not heart-shaped, but lance-shaped with parallel sides.

These points, as indicated by Carr (1952, pp. 366, 377), are characteristic of the Atlantic race of hawksbill, *Eretmochelys i. imbricata*.

(7) Dorsal and sides of head, dorsal of front flippers, and dorsal, distal half of back flippers, all dark black.

This character, as indicated by Carr (1952, p. 366) and Wermuth & Mertens (1961, p. 240), is characteristic of Indo-Pacific hawksbills (*E. i. bisssa (squamata)*).

In regard to other features of lepidosis this specimen fits perfectly with the description in Loveridge & Williams (1958, p. 487) with the following exceptions or optional conditions: no inter-anal; inter-parietal present; top post-ocular continuous with temporal.

*(d) Food*

The intestine of specimen 1 contained large quantities of sponge; more detailed analysis is in progress.

*(e) Symbionts*

† Specimen 2: large area of 'Lithothamnion type' red encrusting algae on posterior half of plastron; large area of filamentous red algae in groin; amphipods and three small barnacles present.

† Specimens 3 and 4: green algae on carapace.

*(f) Discussion*

It seems that specimens 2 to 4 are subadults, and 1 and 5 may be adults, for the smallest breeding female observed in Yemen had a carapace straight length of 63.5 cm (F.A.O. 1967, p. 22). The smallest breeding female in Costa Rica reported by Carr, Hirth & Ogren (1966, p. 5) was 75 cm, and in Guyana the smallest recorded by Pritchard was 80 cm carapace straight length (1969, p. 132). Thus, the sex determinations for the three subadults are questionable, as secondary sex differences are probably not conspicuous at that size. The scale characteristics of specimen 1 make one wonder about the validity of the subspecific division in this species; six characters are aligned with the Atlantic race while one is aligned with the Indo-Pacific race. The most conservative stand at this point is to drop the subspecies designation until further work is done on large series from many localities.

Carr *et al.* (1966, p. 4) and Hirth (F.A.O. 1967) state that hawksbills in the Caribbean and Gulf of Aden are encrusted with barnacles more heavily than the green turtles from these

† Data from J. Gamble & R. Hughes (personal communication).

areas. Pritchard (1969, p. 132,) working in Guyana, makes a similar comment. This situation seems to be reversed at Aldabra, where *Chelonia* is often very heavily encrusted and *Eretmochelys* apparently much less so.

The problem of population size and movements of hawksbills at Aldabra is still very open. Hornell (1927, p. 11) points out that there are far fewer hawksbills, per unit area, at the outlying islands (including Aldabra) than at the Seychelles proper. It also seems, from the Seychellois turtlemen, that the Seychelles animals are much larger than those from the outlying islands. Certainly, very few individuals of this species were harpooned at Aldabra from January to July 1968—I know of only two. Few were seen at sea and there was no sign of breeding. However, it seems that many dozens were captured after my departure in July.

This dramatic change in numbers of animals captured may have been due to two factors. First, the hunting pressure from the Seychellois may have intensified. This seems very likely, for in August 1968 it became illegal to capture green turtles and it appears that the turtlemen then transferred their attention from the highly profitable green turtle to the less profitable hawksbill.

Secondly, there may also have been a change in the turtles' habits or availability. Hornell (1927, p. 14) states that the breeding season for this species is from July to December—peaking from September to November. Coming into breeding condition could obviously result in a change of habits. There is also the problem of migration in the hawksbill at Aldabra. Although Hornell (1927, p. 18) is somewhat sceptical about the existence of a migration in this species, Voeltzkow (1897, p. 18) states that it is 'not uncommon during the egg-laying season, but otherwise only visits the island now and again'—thus indicating a build up of numbers during the breeding season. It should also be pointed out that Carr *et al.* (1966, p. 22) feel that migration occurs in Caribbean hawksbills.

Also related to the problem of population size and movements is the question of a permanent population. Hornell (1927, p. 10) asserts that there is, in the lagoon at Aldabra, a resident population which is characterized by having a light coloured shell. Certainly, the records of sightings indicate that hawksbills are in the lagoon round the year, but, until it has been shown that the *same* individuals are resident, it will be difficult to confirm this suggestion.

In order to get some idea of possible changes in population size over the past 70 years, I have examined the data on annual export of 'tortoiseshell' from Mahé; these data appear in figure 43. It must be emphasized that, to estimate the changes of population size from these data, several assumptions must be made: (1) Annual export must be proportional to annual catch; that is, catches for several years must not have been hoarded and then all sold in one year (as seems to have been the case from 1914 to 1919). (2) The hunting pressure must remain relatively constant. As it is likely, however, to be influenced by current market values, I have included the value of 'tortoiseshell' (rupees/kg) for each year as a rough index of hunting pressure. (3) The proportion of animals captured to the total population must remain constant each year. (4) The average yield of shell per individual should remain constant.

Even *if* these assumptions are valid, figure 43 is difficult to interpret; if they are not, it is almost impossible. Annual export follows a trend similar to annual value, although the correlation is not statistically significant ( $r = 0.216$ ;  $p > 0.05$ ). This suggests that annual 'catch' may be dependent, at least in part, on 'hunting pressure' (i.e. annual value). The latter index has a marked downward trend over the 74 years (regression coefficient =  $-0.3496$ ;  $F = 41.0$ ;  $p < 0.001$ ). Nevertheless, there is no indication that there has been a significant downward

trend in the annual 'catch' (regression coefficient =  $-5.096$ ;  $F = 2.29$ ;  $p > 0.10$ ). The conclusion, *if* the assumptions are correct, is that the number of hawksbills has not decreased since the latter part of the last century.

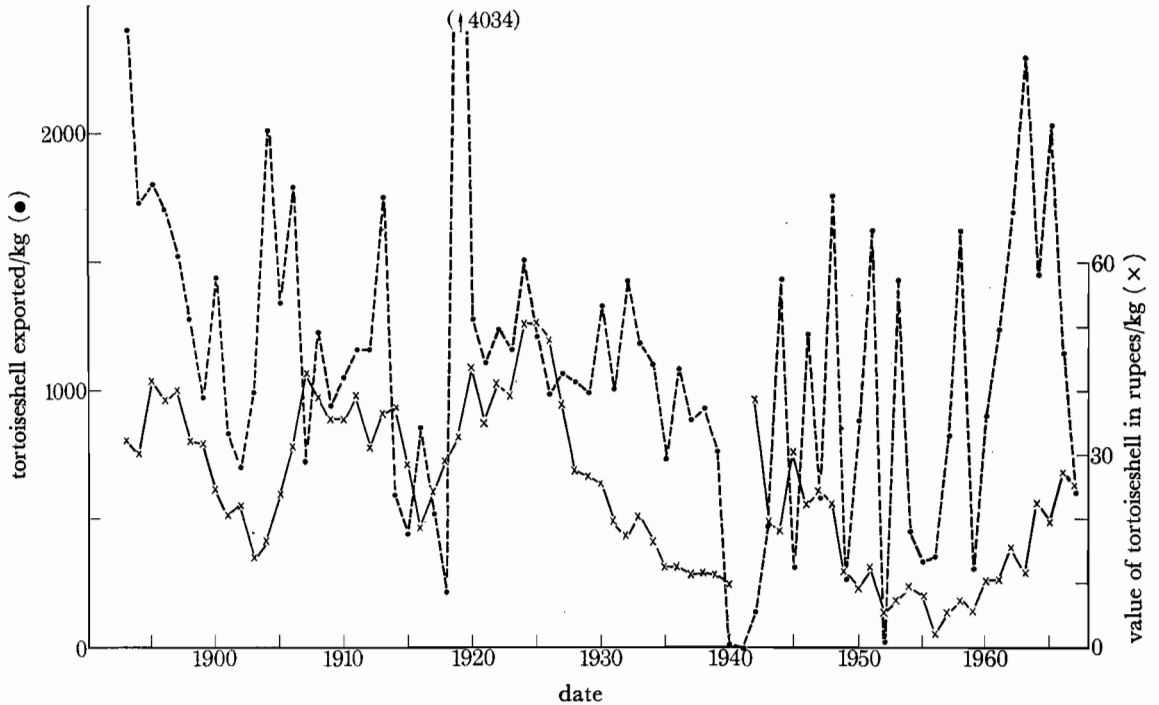


FIGURE 43. Tortoiseshell export data. Data from Hornell (1927, p. 13) for 1893 to 1925; Colonial Reports, Annual, Seychelles (1926 to 1932) for 1926 to 1932; Lionnet (personal communication) for 1933 to 1967. (●---●). Tortoiseshell exported: (×---×) Tortoiseshell value.

Strangely enough, some 70 years ago, Spurs (1892) claimed that hawksbills had diminished in numbers; Hornell (1927, p. 14), however, using many of the same figures that I have, came to a conclusion similar to mine. His conclusion was contrary to popular opinion, and it does seem strange that there has been no decline over the past 70 years. It may be that the interpretation of these data is badly at fault; or it may be that, by chance, the hawksbills are not being over-exploited. Only long-term studies will be able to confirm this.

## 5. LOGGERHEAD *CARETTA CARETTA* L.

### (a) Occurrence

Two authors indicate that this species occurs in the Aldabra area (Hornell 1927, p. 6; Fryer 1911, p. 422). Hornell states that it occurs occasionally in the Seychelles administrative area, but does not breed there. However, later authors (e.g. Carr 1952; Deraniyagala 1939; Loveridge & Williams 1957) do not include Seychelles in the range or locality records for this species—indicating that its occurrence there is questioned. Furthermore, I can find no evidence of any specimen of *Caretta* from the Seychelles being deposited in any of the museums listed on pp. 374–5. Thus, the occurrence of a loggerhead at Aldabra on 11 June 1968 appears to be the first substantiated record of the species for this locality.

Data from this individual are as follows:

| 1. Measurements          |      |        |       |
|--------------------------|------|--------|-------|
|                          | cm   |        |       |
| carapace straight length | 66.5 |        |       |
| carapace curved length   | 70.5 |        |       |
| carapace straight width  | 55.5 |        |       |
| carapace curved width    | 66.0 |        |       |
| plastron length          | 50.5 |        |       |
| head width               | 13.7 |        |       |
| 2. Scalation             |      |        |       |
|                          | left | median | right |
| pre-frontals             | 2    | 0      | 2     |
| postoculars              | 3    | —      | 3     |
| precentrals              | —    | 1      | —     |
| centrals                 | —    | 5      | —     |
| postcentrals             | 1    | 0      | 1     |
| laterals                 | 5    | —      | 5     |
| marginals                | 12   | —      | 12    |
| infra-marginals          | 3    | —      | 3     |
| intra-gular              | —    | 0      | —     |
| gulars                   | 1    | —      | 1     |
| humeral s                | 1    | 0      | 1     |
| abdominals               | 1    | 0      | 1     |
| femorals                 | 1    | 0      | 1     |
| anals                    | 1    | 0      | 1     |
| intra-anal               | 0    | 1      | 0     |

See figures 39 and 40, plates 28 and 29.

### 3. Osteology

In general the condition of the skull fits with the description in Loveridge & Williams (1957, p. 490). The frontal, however, is not excluded from the orbit but contributes about 2 mm to its border. The characteristic vomer, separated from the premaxillae, is illustrated in figure 41, plate 29.

### 4. Scars and wounds

The tail was stubbed to just posterior to the cloaca. Otherwise, this animal was in very good condition, for both front and back flippers were undamaged and the carapace and plastron were undamaged except for two small 3 cm scrapes.

### 5. Symbionts

Thirty-eight large barnacles (*Chelonibia?*) were on the carapace; and about 300 small barnacles (sp?) on the appendages and plastron (J. C. Gamble, personal communication). A 61 cm *Remora* was reported to have been attached to the carapace. Green algae were growing on both carapace and plastron.

### 6. Stomach analysis

J. D. Taylor has identified the following: 1 hermit crab, *Brachiodontes variabilis* and mussels, *Dardanus* sp. The intestine was crammed with mussels.

### 7. Internal organs

The ovaries were recognizable but very poorly developed. Other organs appeared 'normal'. No internal parasites were seen.



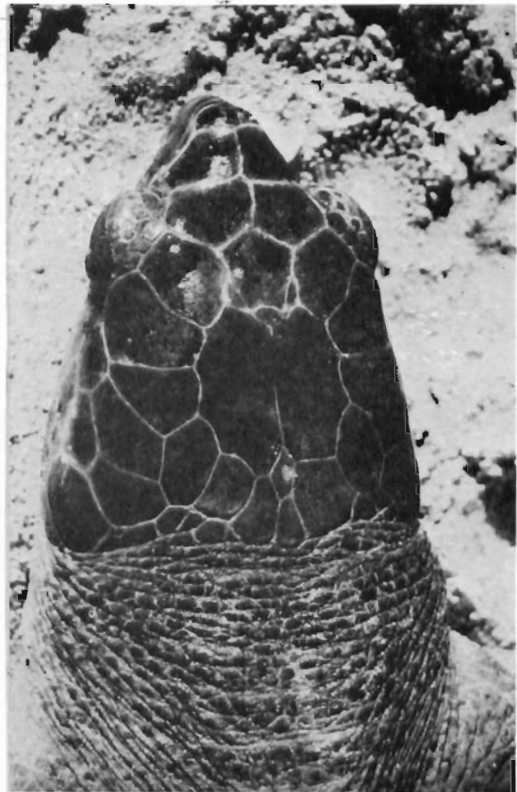
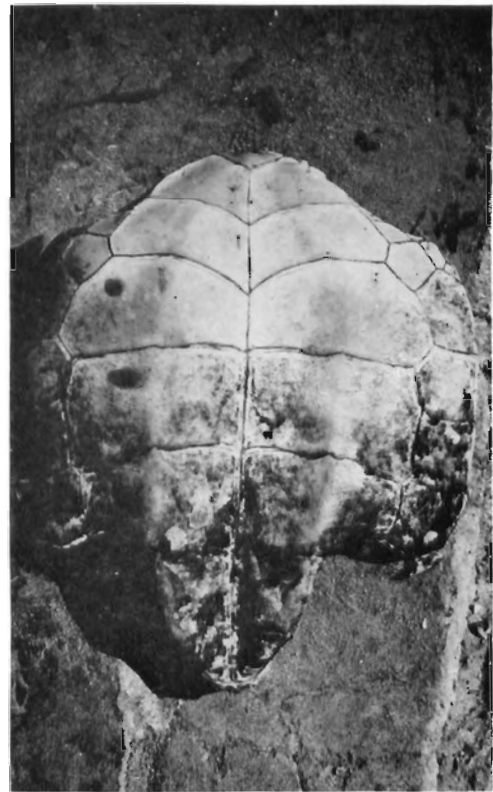
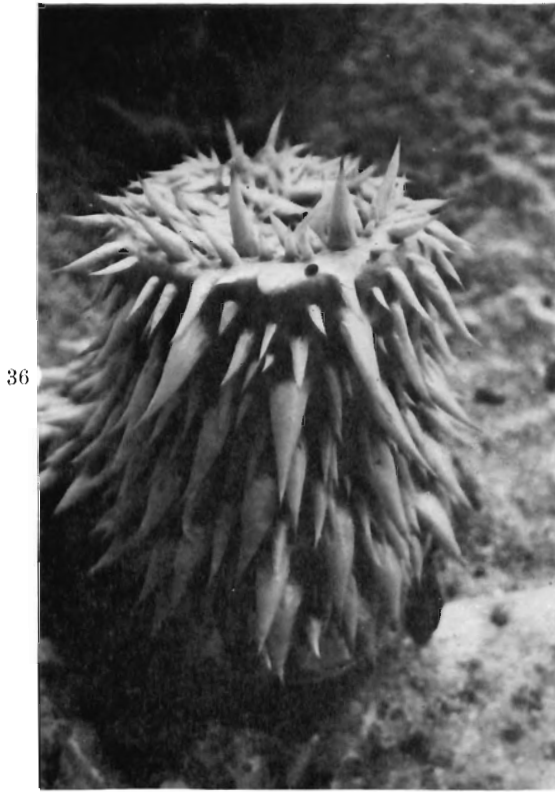


FIGURE 36. Oesophagus of adult male green turtle showing horny papillae.

FIGURE 37. Plastron of hawksbill showing poorly developed keels.

FIGURE 38. Carapace of hawksbill showing: lance-shaped outline, deep serration, and poorly developed median and other keels.

FIGURE 39. Head scales of the loggerhead taken at Aldabra.

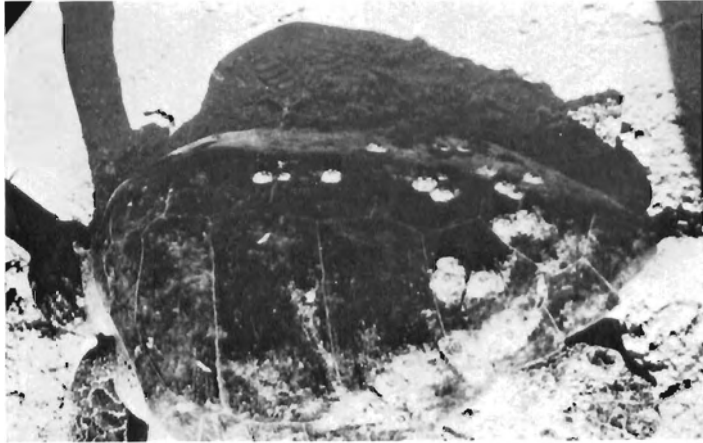


FIGURE 40. Carapace of the loggerhead taken at Aldabra.

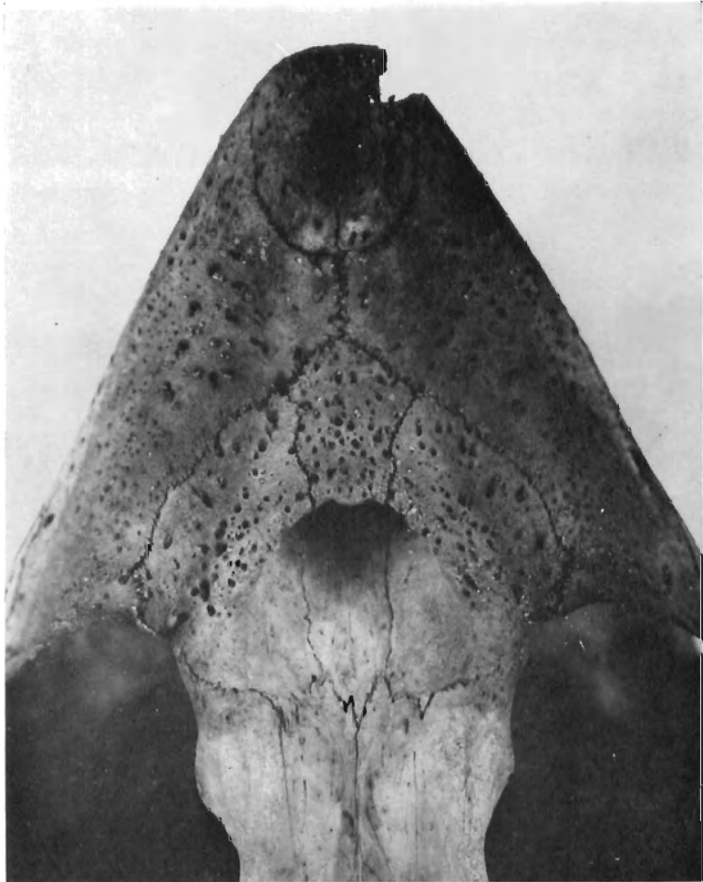


FIGURE 41. Ventral aspects of loggerhead palate showing vomer separated from premaxillae.

(b) *Discussion*

The smallest breeding loggerhead recorded from Tongaland by Hughes, Bass & Mentis (1967, p. 18) was 79 cm curved length of carapace; the smallest breeding female from Georgia recorded by Caldwell, Carr & Ogren (1959, p. 305) was 73 cm straight length of carapace. Thus, both measurements and the condition of the gonads indicate that the animal captured at Aldabra was a subadult. The scalation of this individual is in accord with the modal situation found by Hughes *et al.* (1967), Hughes & Mentis (1967), and Hughes (in press) in Tongaland. The situation with symbionts is also curious, for out of 70 turtles examined in detail at Aldabra, only one, the loggerhead, was found to harbour burrowing barnacles in the carapace. Hughes *et al.* (1967, p. 27) found burrowing barnacles common in the carapaces of nesting loggerheads in Tongaland. As the closest known loggerhead breeding ground to Aldabra is Tongaland, and as the Aldabran individual bears so many similarities to the Tongaland animal, it seems likely that this individual came from Tongaland.

The occurrence of this animal at Aldabra is of relevance in assessing theories concerning movement and dispersal of the species. Hughes (in press), after 6 years work on *Caretta* in Natal, has postulated several means of dispersal for hatchlings. One such is: the hatchlings are picked up by the south-bound Agulhas Current; on reaching 24° E they are swept into the Indian Ocean Gyral; they then take up a pelagic existence for several years. If, in fact, Natal is the origin of the Aldabran loggerhead, then its movements fit well with Hughes's hypothesis.

## 6. OTHER SPECIES

(a) *Ridley* *Lepidochelys olivacea*

Deraniyagala (1939, p. 163) lists Seychelles in the locality records of this species but I can find no evidence for its occurrence.

(b) *Leatherback* *Dermodochelys coriacea*

There are apparently no locality records for this species in Seychelles; but it seems, from the descriptions of the turtlemen, that it does occur, but very rarely.

## 7. RELATIONSHIP TO MAN

(a) *The turtlemen's accounts*

The Seychellois turtlemen have a good working knowledge of sea turtles, and, although many of their beliefs are unfounded, many are consistent with our present knowledge.

*Nomenclature*

## 1. Species

| Creole                                                      | English                       | Latinized                     |
|-------------------------------------------------------------|-------------------------------|-------------------------------|
| Tortue or Tortue de mer                                     | Green Turtle or Edible Turtle | <i>Chelonia mydas</i>         |
| Caret                                                       | Hawksbill                     | <i>Eretmochelys imbricata</i> |
| Name Coyio<br>(also Tortue batarde<br>(Hornell 1927, p. 6)) | Loggerhead                    | <i>Caretta caretta</i>        |
| †                                                           | Ridley                        | <i>Lepidochelys olivacea</i>  |
| † Tortue Carembol                                           | Leatherback                   | <i>Dermodochelys coriacea</i> |

† Note: no specimens of these species were seen on Aldabra.

## 2. Scales

| Creole       | English                                                                    |
|--------------|----------------------------------------------------------------------------|
| Col          | Pre-central                                                                |
| Coupier      | Post-centrals                                                              |
| Feuille      | Laterals and centrals                                                      |
| Ongles longs | Marginals                                                                  |
| Plastron     | Plastron                                                                   |
| Rupce        | Large round scale on ventral of front flipper of green turtle; also a coin |

## 3. Other

| Creole    | English                   |
|-----------|---------------------------|
| Bernique? | Barnacles                 |
| Graban    | Barnacles                 |
| Vers      | Leeches                   |
| Batailler | To court (to fight)       |
| Coplase   | Copulation                |
| Maquereau | Extra males around a pair |

*General biology*

1. *Green Turtle*. This species is said to commute freely between Aldabra, Assumption, Cosmoledo and Astove. A female breeds several times a year and then goes away for a long time. Vision is poor and sense of smell good; they can hear a boat coming if the oars are banged. They will not nest on a beach where there are lights, nor on badly surf-beaten beaches, but will go to another island. Unlaid, shelled, eggs from a slaughtered female will hatch if buried. Hatchlings are said to be preyed on by everything imaginable.

2. *Hawksbill*. It breeds on lagoon islands at Aldabra; its meat is poisonous and is discarded, although the calipee is kept. If, however, a piece of silver or gold is placed in the muscle for several minutes and does not tarnish, then the meat is safe to eat.

3. *Loggerhead*. A 'mule' which never breeds and is a hybrid between the green turtle and hawksbill. If the loggerhead is large, then the mother was a green; if it is small, then the mother was a hawksbill. Its meat is not relished.

4. *Ridley*. This may occur.

5. *Leatherback*. Very rarely seen; it seems to occur in Seychelles. Named after a certain fruit (Carembol) which it resembles in texture.

*(b) Economic importance*1. *Green Turtle*

The green turtle is an extremely important source of protein—some 50% or more of its mass being wholesome meat (Deraniyagala 1939, p. 222; F.A.O. 1967, p. 16). On Aldabra, before the total protection of this species, meat was consumed by the Seychellois in approximately weekly rations. Some meat was salted and dried (to produce 'quitouze') and flippers were salted for dried ('fins'). Both of these products are exported for consumption in Seychelles and in foreign countries. Calipee (a type of cartilage) is at present the most financially important product from the green turtle. It is rarely, if ever, consumed in the Seychelles legislative area, being saved for export. At present, there is no apparent effort to market turtle oil, turtle bone fertilizer, or green turtle shell, as was done in the earlier part of this century.

Unshelled 'yolk' eggs from a slaughtered female are eaten, as are shelled eggs both from slaughtered females and from nests (Gaymer, personal communication); the last source of eggs is illegal. There is no legal commercial exploitation of turtle eggs. The only other item of value

is the cleaned carapace which is occasionally used as a basin for holding fish bait or salting meat. In addition to these various turtle parts, live turtles are shipped to Mahé.

Thus, the green turtle in the Seychelles is important as: a source of meat for local consumption; calipee for foreign export; whole animals, dried meat, and fins for export and local consumption; small amounts of eggs for local consumption; and the occasional fish basin.

The green turtle industry is extremely wasteful (Hornell 1927, p. 35). Animals that are slaughtered at outlying camps on Aldabra are not utilized to the fullest possible extent; often only the calipee and a small proportion of meat are taken, with a tremendous amount of fine meat being wasted. Animals that are slaughtered in the settlement are utilized much more fully, but Hornell (1927, p. 29) states that production of quitouze (dried meat) must be very wasteful—turning a 'magnificent animal' into 'an insignificant amount of badly-cured dry flesh'. There is also tremendous wastage in the shipping of live turtles. On one occasion three out of 30 animals died on board the ship overnight—before she even got under way! Hornell (1927) claims that as many as 50 % of the turtles shipped alive may die *en route*, and Voeltzkow (1897) also mentioned this problem. Turtles that are kept, often for months, in the shallow turtle pen at Aldabra are rarely, if ever, able to feed, and then only a few sprigs of mangrove (*Rhizophora*) thrown in by the turtlemen are available. Not only are animals forced to subsist solely on their own body tissues while in the pen, but the conditions are so bad that many animals are very unhealthy. One male had the entire length of its caudal vertebrae exposed with the associated tissues literally rotting away.

In short, the green turtle fishery has not only been over-exploiting its resource toward extermination, but it has been exploiting it in an extremely wasteful manner.

## 2. *Hawksbill*

The hawksbill is taken for its epidermal shields, 'tortoiseshell'. In obtaining these shields the animal is slaughtered (there is apparently no attempt to remove the shield from a live animal and return it to the sea, as is done in other parts of the world (see Carr 1952, p. 371, and Deraniyagala 1939, p. 189). Other than the epidermal shields, the only other items of value from a hawksbill are a few small pieces of calipee; the rest of the animal is discarded. This is because the meat is thought to be poisonous. In fact, Deraniyagala (1939, p. 190) and Carr (1952, p. 371) state that poisonous meat does occur in this species, but there is no indication that *every* individual is poisonous.

Again, the exploitation of this species is very wasteful. The meat is occasionally poisonous but this does not warrant large-scale wastage which does occur. It would be in the best interests of the Government and the people of Seychelles to develop a simple test for determining the edibility of meat from this species.

## 3. *Other species*

Apparently neither sufficient ridleys nor leatherbacks are taken in the Seychelles area to warrant any discussion of them under economic importance. The loggerhead is possibly in the same category, but there are not enough data to tell at this point. The only item utilized from the loggerhead was its calipee; the epidermal shield, meat, internal organs—in fact the entire remainder of the animal—was discarded. This was done because the meat is not liked, but there is no indication from any locality that loggerhead meat is inedible. If these animals are to be slaughtered for a few strips of calipee, then the meat should be utilized as well.

*(c) Conservation*

Many authors (Fryer 1911; Hornell 1927; Wheeler 1953; Veevers-Carter 1962; Gaymer 1966; Honegger 1967; Hirth, F.A.O. 1967) have examined the status of the green turtle in the Seychelles area and have strongly recommended immediate and comprehensive measures for conservation. It can be seen from the section dealing with population size that there is considerable substance in the unanimous recommendation by these authors; the green turtle has declined dramatically over the past century at Aldabra. The enactment of a law in August 1968 made it illegal to catch green turtle.

The hawksbill appears to be in a slightly different position for two reasons. First, its importance, and thus the hunting pressure, is probably dependent on numerous variables—it is of no direct value as a source of food. Secondly, there is at present no indication that its numbers have been declining over the past 70 years; although it should also be pointed out that there is no good information for refuting any decline in the population.

Nevertheless, an effort must be made to avoid over-exploitation of this species and the consequent ruining of the tortoiseshell fishery. Accurate records of numbers, sex, and sizes of animals taken should be kept, and these will enable intelligent cropping schemes to make the most of the resource for long term exploitation.

A great number of people have helped in gathering and analysing the data presented. I am grateful to all expedition members who have contributed information and assistance—especially: J. C. Gamble, R. Hughes, A. Hutson, R. Lowery, J. M. Lythgoe and A. G. Yeates. The manager and turtlemen on Aldabra were very helpful. Determinations of symbionts and food items have been made by: C. A. Wright (internal parasites), B. H. Cogan (insects), W. Smith (barnacles), J. C. Gamble (barnacles), J. D. Taylor (food items).

Colleagues at Oxford have assisted in discussions. B. MacRoberts, M. MacRoberts, J. Smith, and L. Shaffer gave generously of their time in evaluating colour slides. G. Hughes of Durban has also assisted in this respect. Museum curators have kindly given me information and hospitality. I am especially grateful to N. Arnold at the British Museum. R. Honegger, Zurich, generously provided me with tagging equipment and also raw data from Aldabra. B. E. Bell kindly sent me length and mass data of Aldabra hatchlings kept in captivity. G. Lionnet, Mahé, provided me with turtle records from Seychelles.

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The work was done while on the Royal Society Expedition and I am grateful to this organization and the many people involved.

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## REFERENCES (Frazier)

- Balasingham, E. 1965 Conservation of Green Turtles (*Chelonia mydas*) in Malaya. *Malay. Nat. J.* **19**, 235–236.  
 Balasingham, E. 1967 Turtle conservation: results of 1965 hatchery programme. *Malay. Nat. J.* **20**, 139–141.  
 Caldwell, D. 1962a Growth measurements of young captive Atlantic sea turtles in temperate waters. *Contr. Sci.* **50**, 1–8.

- Caldwell, D. 1962*b* Sea turtles in Baja California Waters (with special reference to those of the Gulf of California), and the description of a new sub-species of North-eastern Pacific green turtle. *Contr. Sci.* **61**, 1-31.
- Caldwell, D. 1962*c* Carapace length-body weight relationship and size-sex ratio of the North-eastern Pacific green turtle, *Chelonia mydas carrinegra*. *Contr. Sci.* **62**, 1-10.
- Caldwell, D., Carr, A. & Ogren, L. 1959 Nesting and migration of the Atlantic Loggerhead Turtle. *Bull. Fla. State Mus.* **10**, 295-308.
- Carr, A. 1952 *Handbook of Turtles*. Ithaca: Cornell University Press.
- Carr, A. 1956 *The windward road*. New York: A. A. Knopf.
- Carr, A. 1965 The navigation of the Green Turtle. *Scient. Am.* **212**, 79-86.
- Carr, A. 1967 *So Excellent a Fish*. New York: Natural History Press.
- Carr, A. & Caldwell, D. 1956 The ecology and migrations of sea turtles. 1. Results of field work in Florida, 1955. *Am. Mus. Novit.* **1793**, pp. 23.
- Carr, A. & Giovannoli, L. 1957 The ecology and migrations of sea turtles. 2. Results of field work in Costa Rica, 1955. *Am. Mus. Novit.* **1835**, pp. 32.
- Carr, A. & Hirth, H. 1962 The ecology and migrations of sea turtles. 5. Comparative features of isolated Green Turtle colonies. *Am. Mus. Novit.* **2091**, pp. 42.
- Carr, A., Hirth, H. & Ogren, L. 1966 The ecology and migrations of sea turtles. 6. The Hawksbill Turtle in the Caribbean Sea. *Am. Mus. Novit.* **2248**, pp. 29.
- Carr, A. & Ogren, L. 1960 The ecology and migrations of sea turtles. 4. The Green Turtles in the Caribbean Sea. *Bull. Am. Mus. nat. Hist.* **121**, 1-48.
- Cousteau, J. 1963 *The living sea*. London: Hamish Hamilton.
- Croze, H. J. 1967 Dispersion in camouflaged animals and searching image in predators. D.Phil. Thesis, University of Oxford.
- Deraniyagala, P. 1939 *Tetrapod reptiles of Ceylon*. London: Dulau.
- Ehrenfeld, D. 1968 The role of vision in the sea-finding orientation of the Green Turtle (*Chelonia mydas*). 2. Orientation mechanisms and range of spectral sensitivity. *Anim. Behav.* **16**, 281-287.
- Ehrenfeld, D. & Carr, A. 1967 The role of vision in the sea-finding orientation of the Green Turtle (*Chelonia mydas*). *Anim. Behav.* **15**, 25-36.
- F.A.O. 1967 Report to the Governments of Southern Yemen and the Seychelles Islands on the green turtle resource of South Arabia, and the status of the green turtle in the Seychelles Islands. Based on the work of Dr H. F. Hirth, F.A.O./T.A. Marine Turtle Biologist. *Rep. F.A.O./U.N.D.P. (TA)*, (2467).
- Fryer, J. 1911 The structure and formation of Aldabra and neighbouring islands—with notes on their flora and fauna. *Trans. Linn. Soc. Lond.*, ser. 2, Zool. 14 (Percy Sladen Expedition Reports, 3) 397-442.
- Gaymer, R. 1966 The green turtle *Chelonia mydas japonica* (Thunberg) in the Seychelles, Amirantes and Aldabra group. Mimeographed, 1-7.
- Goin, C. & Goin, O. 1962 *Introduction to herpetology*. London: Freeman.
- Graham, A. 1969 The Lake Rudolph Crocodile. M.A. Thesis, University of East Africa.
- Harrison, T. 1954 The edible turtle (*Chelonia mydas*) in Borneo. 2. Copulation. *Sarawak Mus. J.* **6**, 126-128.
- Harrison, T. 1955 The edible turtle (*Chelonia mydas*) in Borneo. 3. Young in Captivity. *Sarawak Mus. J.* **6**, 633-640.
- Harrison, T. 1956 The edible turtle (*Chelonia mydas*) in Borneo. 5. Tagging turtles and why. *Sarawak Mus. J.* **7**, 504-515.
- Hendrickson, J. 1958 The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Proc. Zool. Soc. Lond.* **130**, 455-535.
- Honegger, R. 1967 The Green Turtle (*Chelonia mydas japonica* Thunberg) in the Seychelles Island. *Br. J. Herpet.* **4**, 8-11.
- Hornell, J. 1927 *The turtle fisheries of the Seychelles Islands*. London: H.M.S.O.
- Hughes, G. (In press) Further studies on Marine Turtles in Tongaland. III.
- Hughes, G., Bass, A. & Mentis, M. 1967 Further studies on Marine Turtles in Tongaland. I. *Lammergeyer* **7**, 5-54.
- Hughes, G. & Mentis, M. 1967 Further studies on Marine Turtles in Tongaland. II. *Lammergeyer* **7**, 55-72.
- Krummel, D. In Werner, F. 1912 Die Lurche und Kriechtiere. In Brehm, A. *Tierleben*. Leipzig. Cited by Love-ridge & Williams 1957, p. 481.
- Loveridge, A. & Williams, E. 1957 Revision of the African tortoises and turtles of the Suborder Cryptodira. *Bull. Mus. Comp. Zool.* **115**, 163-557.
- Moorehouse, F. 1933 Notes on the Green Turtle (*Chelonia mydas*). *Rep. Gt Barrier Reef Comm.* **4**, 1-22.
- Ommanney, F. 1949 *The shoals of Capricorn*. London: Longmans Green.
- Parsons, J. 1962 *The green turtle and man*. Gainesville: University of Florida Press.
- Phillips, R. C. 1960 Observations on the ecology and distribution of the Florida sea grasses. *Prof. Pap. Ser. mar. Lab. Fla.* no. 2.
- Pritchard, P. 1967 *Living turtles of the world*. Jersey City: T.F.H. Publications.
- Pritchard, P. 1969 Sea turtles of the Guianas. *Bull. Florida State Mus.* **13**, 85-140.

- Randall, J. E. 1965 Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* **46**, 255–260.
- Schmidt, 1916 Marking experiments with turtles in the Danish West Indies. *Meddr Kommn Havunders., ser. Fiskeri* **5**, 1–26. Cited by Hornell 1927, p. 40.
- Sheppard, P. M. 1958 *Natural selection and heredity*. London: Hutchinson University Press.
- Spurs, J. 1892 (Report on Aldabra to T. Risely Griffiths, Esq., Administrator of Seychelles Islands. Port Victoria, Seychelles, 19 July 1891.) Colonial Reports—Annual No. 40. Mauritius (Seychelles and Rodriguez). Annual Reports for 1889 and 1890, with a report on the island of Aldabra. 46–50. London: H.M.S.O.
- Travis, W. 1959 *Beyond the reefs*. New York: Dutton.
- Veevers-Carter, M. 1962 The development of the green turtle (*Chelonia mydas*) fisheries of the Seychelles. Mahé: Department of Agriculture, report.
- Voeltzkow, A. 1897 Einleitung; Madagaskar, Juan de Nova, Aldabra. *Abhand. Senckenb. naturf. Gesellsch.* **21**, 1–76. Aldabra, Indischer Ocean 1895, pp. 40–73 (mimeographed translation from D. R. Stoddart).
- Voeltzkow, S. 1913 In Boettger, O. Reptilien und Amphibies von Madagaskar, des Inseln und dem Festland Ostafrikas. In Voeltzkow, A. 1913 *Reise in Ostafrika in den Jahren 1903–1905*, Band III, Heft IV.
- Wermuth, H. & Mertens, R. 1961 *Schildkröten. Krokodile. Brückenechsen*. Jena: Gustav Fisher.
- Wheeler, J. 1953 Memorandum on the green turtles (May 12, 1948). Appendix 5, 143–145. In Wheeler & Ommaney 1953, Report on the Mauritius–Seychelles Fisheries Survey, 1948–1949. *Colonial Fisheries Research Publications*, **1** (3), 1–145.

*Colonial Reports, Annual. Seychelles. 1926 to 1932*. London: H.M.S.O.

#### APPENDIX I. ESTIMATION OF PLANT FOOD BIOMASS AT ALDABRA AND ITS CARRYING CAPACITY

(1) Biomass per area (dry mass):

$$(A) = 2897 \text{ lb dry } Thalassia \text{ leaves/acre (Phillips 1960).}$$

Conversion to metric:

$$(B) = (A) (0.4359) (247.1) = 312\,038.45 \text{ kg dry leaves/km}^2.$$

(2) Biomass per area (wet mass):

85 % of leaf mass is water (Phillips 1960).

$$(C) = (B)/(0.15) = 2\,080\,256.32 \text{ kg wet leaves/km}^2.$$

(3) Biomass at Aldabra:

11.875 km<sup>2</sup> of prime *Cymodocea/Thalassia* at Aldabra (from Taylor, in preparation).

$$(D) = (C) (11.875) = 24\,703\,043.56 \text{ kg wet leaves in prime habitat at Aldabra.}$$

Productivity of 'dense algae' is not known; at Aldabra it grows at roughly the same density and concentration as the *Cymodocea/Thalassia*, but occupies only about half the area. Thus, it could be estimated that an additional  $\frac{1}{2}(D)$  kg of wet leaves is present in 'dense algae'. Again, for the reef platform there are no figures for productivity. The reef platform consists of an area roughly twice that of the *Cymodocea/Thalassia*; however, the overall concentration of plants on the reef platform is much less (possibly  $\frac{1}{4}$ ) than in the other two habitats. Another quantity of  $\frac{1}{2}(D)$  kg of wet leaves could be added for the reef platform (data on area of various habitats from Taylor, in preparation).

$$(E) = (D) (2) = 49\,406\,087.12 \text{ kg wet leaves at Aldabra.}$$



## (4) Feeding requirements:

2.25 kg (10 lb) wet *Posidonia*/stomach (Hirth, F.A.O. 1967). Stomach emptied in less than 12 h (Deraniyagala 1939). Estimate two stomach-fulls/day/turtle = 4.5 kg wet leaves/day/turtle.

## (5) Number of turtle days possible at Aldabra on standing crop:

$$(F) = (E)/(4.5) = 10979130 \text{ turtle days at Aldabra.}$$

## (6) Potential number of migrant breeders/year:

In a season a female lays 3 or 4 nests at two-week intervals (see Breeding biology §3*d*). Estimate 60 days/visit/female/year. Assume males stay for the same length of time.

$$(G) = (F)/(60) = 182986 \text{ migrant breeders/year.}$$

## (7) Potential number of resident turtles:

$$(H) = (F)/(365) = 30080 \text{ residents.}$$

## (8) Potential number of breeding residents:

A female breeds every three years (see references in Breeding biology §3*d*).

$$(J) = (H)/(3) = 10027 \text{ breeding residents/year.}$$

Thus, the number of breeding migrants =  $18 \times$  the number of breeding residents.

*Note:* Estimates are based on standing crop only; no account of plant regeneration has been taken. All plant food is assumed to be eaten by adult green turtles; no account of any other marine grazer has been taken. (See also Feeding §3*l*.)

## POSTSCRIPT

(Added in proof 1 September 1970)

Immediately upon presenting this paper for publication I returned to Aldabra for further field work. Additional data will be presented in a later paper. It is, however, worth pointing out the following:

*Green turtle*

(1) The species certainly breeds throughout the year at Aldabra. The peak in the laying season begins at the commencement of the SE Trades (later than Hornell's (1927) peak). (See p. 375.)

(2) Recent observations indicate that copulation occurs just before a clutch is to be laid—not 3 years before. (See p. 377–8.)

(3) Average clutch size is larger than stated. (See p. 379.)

(4) Detailed observations on number of new nests/month indicate that 1000 nesting females/year is a reasonable estimate. (See p. 393.)

(5) Burrowing barnacles *do* occur on Aldabran green turtles. (See p. 394.)

*Hawksbill*

The presence of animals in varying size classes, but very little breeding, indicates that the Aldabran population is migratory. (See p. 400.)

*Other species*

Mr Kantilal Jivan Shah, Mahé, has shown me definitive photographs of a leathery turtle captured off Mahé some years ago. (See p. 403.)

The Ridley turtle seems unlikely to be known in Seychelles. (See p. 403.)

*Conservation*

At this time it is probable that the protective legislation for the green turtle made effective on August 1968 will be relaxed and possibly repealed.

*Publications*

Two publications relevant to Seychelles have since appeared:

- Hirth, H. & Carr, A. 1970 The Green turtle in the Gulf of Aden and the Seychelles Islands. *Verh. K. ned. Akad. Wet.* 58, 1–44.
- I.U.C.N. 1969 Marine turtles. Supplementary paper no. 20. Proceedings of the working meeting of marine turtle specialists, Morges, Switzerland. 10–13 March 1969.