J. Frazier

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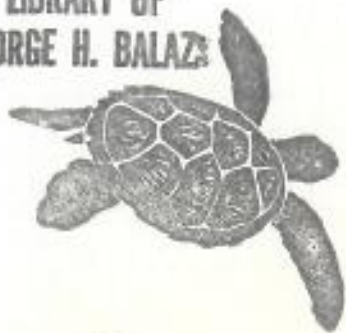
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For Jane

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GENERAL INTRODUCTION

Studies in the Comoro Archipelago form part of a larger project to assess the status and distributions of sea turtles in the western Indian Ocean (Frazier, 1975; 1980b; 1982; Hughes, 1982), an ambitious venture that still continues (Frazier, in prep.). The Comoro Archipelago has been little studied, and the sea turtles there have been virtually ignored by biologists. None the less, there are relatively large numbers of turtles nesting in these islands, and the adjoining shallow water areas, with some of the richest reefs in the western Indian Ocean, may provide important feeding habitats for many turtles. This report is the first detailed account of marine turtles in the Comores. Based on merely four month's observations, it is but a preliminary statement, but because follow-up studies are likely to be few – there have been none in over a decade – the results are presented in detail to facilitate future comparative studies.

The spellings of place names used in the present work are taken from detailed maps of the Institut Géographique National (France, 1958, 1959). As the language spoken in Comores is akin to swahili, it might best be written with an Arabic alphabet. However, being an ex-French colony, local names are spelled in roman script with french phonetics – far from an ideal system – and there are thus numerous alternative spellings for some words, (e.g., the word for '-island' on French maps varies from 'Chissioua' to 'Chissioi' to 'Zissioua' to 'Sisoa'). In addition, some local place names are used for more than one location: there are three beaches called 'M'Sanga Nyamba' on Mohéli Island. To avoid confusion the serial number is also given when referring to beaches.

The methods used for measuring were simple: beach lengths and widths were estimated by pacing all or part of the supralitoral beach platform. Distance from beach crest to nest pit was measured by pacing inland from the crest and recording nearby nest pits. Eggs, collected during laying or from oviducts of nesting females slaughtered by natives, were weighed with a 100 g Pescola spring balance and measured along three perpendicular diameters with vernier calipers. Usually eggs were measured within 24 hours of oviposition, but under heavy work loads measuring was delayed a day. Hatchling turtles were taken from emerging nests and weighed with the spring balance; vernier calipers

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were used for linear measurements. Specimens larger than hatchlings were measured with a flexible tape, over the curve of the shell: curved carapace length (CCL) – the greatest median length from the centre of the cervical to the posterior-most tip of a supracaudal; curved carapace width (CCW) – the greatest width perpendicular to the long axis of the body; plastron length (PL) – the greatest median length, from the anterior-most tip of the intergular to the posterior-most tip of the postanal; head width (HW) – the greatest distance, perpendicular to the long axis of the head, slightly posterior to the two tympana. Names of epidermal scales are as described in Zangerl (1968: 315) with two modifications: the last (posterior) pair of marginals are the 'supracaudals'; the scale posterior to the anals on the plastron is the 'postanal'.

Statistical analyses involving large data matrices were performed at the Office of Computer Services, Smithsonian Institution, using Statistical Package for the Social Sciences (SPSS) release 8.OC-2 (Nie et al., 1975). Specific statistical tests that were used, but not available on SPSS, include the t-test for kurtosis (g2) (Sokal & Rohlf, 1969: 112-118, 137, 171), the G test 'variation' of χ^2 (Sokal & Rohlf, 1969: 599), analysis of covariance (Snedecor & Cochran, 1967: 432 ff.), and the t test for comparing two regression coefficients (Bailey, 1964: 97-99).

The four major islands of the Archipelago form a natural unit; they are geographically and geologically close. Certain aspects of this report must, however, treat the Comoro Archipelago in separate parts. There are political, historical, biological, and management reasons for this division. The Federal and Islamic Republic of the Comores forms a political entity, comprising the islands of Grande Comore (or 'Ngazidia'), Mohéli (or 'Mwali'), and Anjouan (or 'Johanna'). With a culture that is mainly Swahili-Arabic, these three islands have, for the most part, had relatively loose ties with France. Anjouan and Grande Comore are steep-sided, geologically young, and provide little nesting or feeding habitat for marine turtles. They are densely populated and have pressing human problems. Mohéli is distinctive with a significant amount of shallow water and a considerable amount of undisturbed beach habitat. It provides food not only for its own population, but also for those on Grande Comore and Anjouan. Within the Republic only Mohéli is of major importance to marine turtles.

The island of Mayotte forms a second political entity; it is a French Department. Historically Mayotte has had longer and closer ties with France, and people of Malagassy ancestry make up much of the population. This island is a marine paradise with immense and complicated barrier, patch, and fringing reefs, making it unlike any other island in the western Indian Ocean.

A separate treatment of these islands is warranted from the biological evidence. Marine turtles have strong philopatry when nesting, especially the Green Turtle, *Chelonia mydas* (L.), one of the two species that is common in the

Comores. From other studies of island systems (e.g., Hendrickson, 1958) interchanges between islands seem to be rare. The Hawksbill, *Eretmochelys imbricata* (L.), the other common turtle occurring in Comores, is apparently sedentary in habits. Hence, the turtles that occur at the various islands could be considered to be distinct populations. After the separate treatments of the populations at each island, comparisons between the islands are made; as most information is available for Mohéli and Mayotte, this discussion is limited mainly to these two islands.

Conservation and management of marine turtles is an international problem, and many studies of the biology of these animals are needed for rational management of their populations. However, management is also a political issue, for each state must legislate and enforce its own laws. Separate discussions of separate sovereign states is often the most appropriate means to make relevant information available to policy makers. Hence, the final section presents separate recommendations for two political entities.

DESCRIPTION OF THE ARCHIPELAGO

Geography

The Comoro Archipelago includes four major islands: Grande Comore (or 'Ngazidia'), Mohéli (or 'Mwali'), Anjouan (or 'Johanna'), and Mayotte. Between 40 and 60 km apart, these islands rise as isolated sea mounts at the northern end of the Mozambique Channel, east of northern Mozambique on the African mainland and west of northern Madagascar. They lie between 11° 22' and 13° 5' S and from 43° 13' to 45° 18' E (Figure 1), and are flanked to the east by Recif Vailheu and to the west by Banc du Geyser.

The Comores are volcanic in origin, possibly Miocene. Grande Comore, geologically youngest, is dominated by the Kartala Volcano, which had minor eruptions in September/October 1972 and April 1977 (Simkin et al., 1981). It is the largest and highest island, 64 km long by 31 km wide, and covers 950 km² (Figure 2). Kartala rises to 2,361 m. Lava fields and small volcanic cones are conspicuous over the island, notably in the northern half. Grande Comore has a paucity of soil and water; there are no permanent streams. No freshwater lakes exist, but Niamaouy Crater Lake in the extreme north is connected to the sea, and there are several seawater basins on the west coast, south of Iconi vil-

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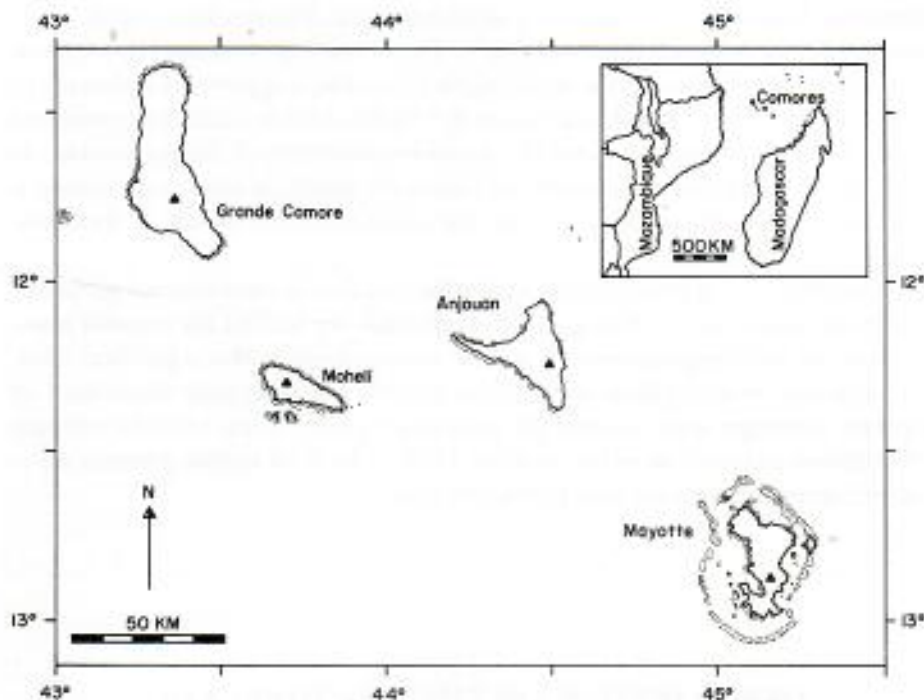
Figure 1   The Comoro Archipelago, showing position in the Mozambique Channel (inset); reefs are indicated by dotted lines, highest point on each island, by a triangle.

lage. The shoulders of Kartala are cloaked in rain forest. Choua–Chandroudé (or Ile aux Tortues) is the only offshore island. It is 300 m off the northwest and about one ha in area.

By contrast, Mohéli Island is smallest and lowest. Only 790 m high, it is 29 km long (northwest to southeast) and 12 km wide, and has an area of 216 km² (Figure 3A). A hogback ridge runs most of the length. There are several permanent streams and ample soil. It is completely vegetated. Much of the lower part is planted in coconut or ylang-ylang (*Cananga odorata* DC.), and the high ground has good forest cover, although in secondary growth. The crater lake Dziani Boundouni is in the southeast. A dozen islands lie off the south and southeast coasts of Mohéli. From east to west they are: Chissioua M'Chaco, C. Gnandza, C. M'Bouzi (east), C. Chikoundou, C. Foro, C. Méa, C. M'Bougo, C. Chandzi, C. Ouénéfou, C. M'Bouzi (south), C. Canzoni, C. Dzaha and C. Magnougni. In the south especially these islands appear as emergent sections of ridges that radiate out from the centre of Mohéli. Chissioua Ouénéfou is longest and highest, over 3 km long and 195 m high. It is also the most important turtle island at Mohéli, and Mohéli is one of the most important turtle islands of the western Indian Ocean.

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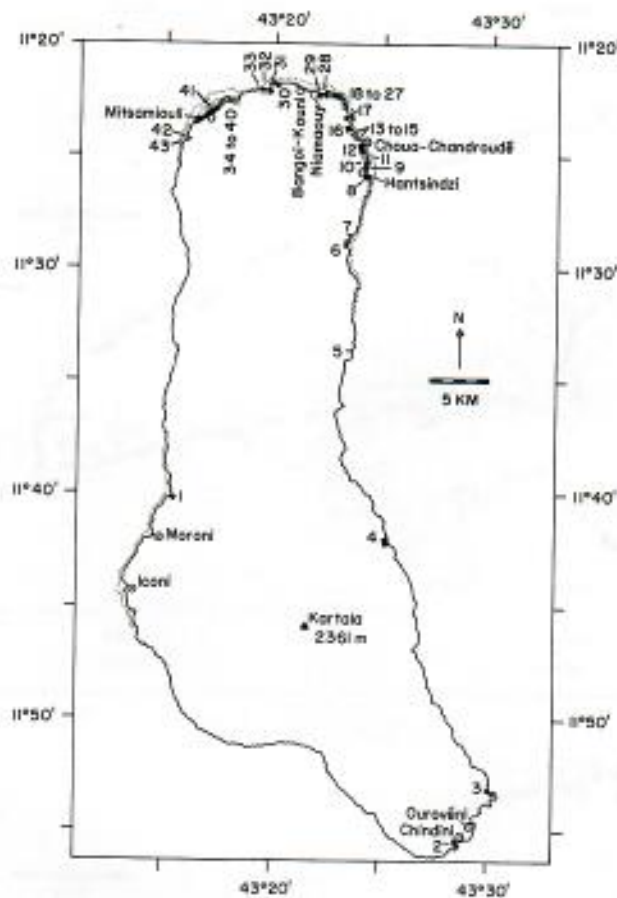
Figure 2   The island of Grande Comore; individual beaches are numbered 1 to 43 (see Table 1 for details); reefs are indicated by dotted lines; Niamaouy crater lake and Choua-Chandroudé island are shown in the northeast; towns mentioned in the text are shown by open circles.

Anjouan is often said to be the most beautiful of the Comoro Islands. Shaped like a triangle, its north-south side is 35 km long, and the east-west dimension is 37 km: the area is 378 km² (Figure 4). N'Tingui, near the centre of the island, rises to 1,595 m. Three major ridges radiate out from this point to the three angles of the triangle. The island has ample soil and is well watered. There are numerous permanent streams and two small crater lakes near the centre. It is completely vegetated, but much of the island is covered in coconut, ylang-ylang, vanilla, cloves and other export crops. Even the steep upper slopes are cultivated. Some rain forest is left in the Forêt de Moya, toward the south. There are

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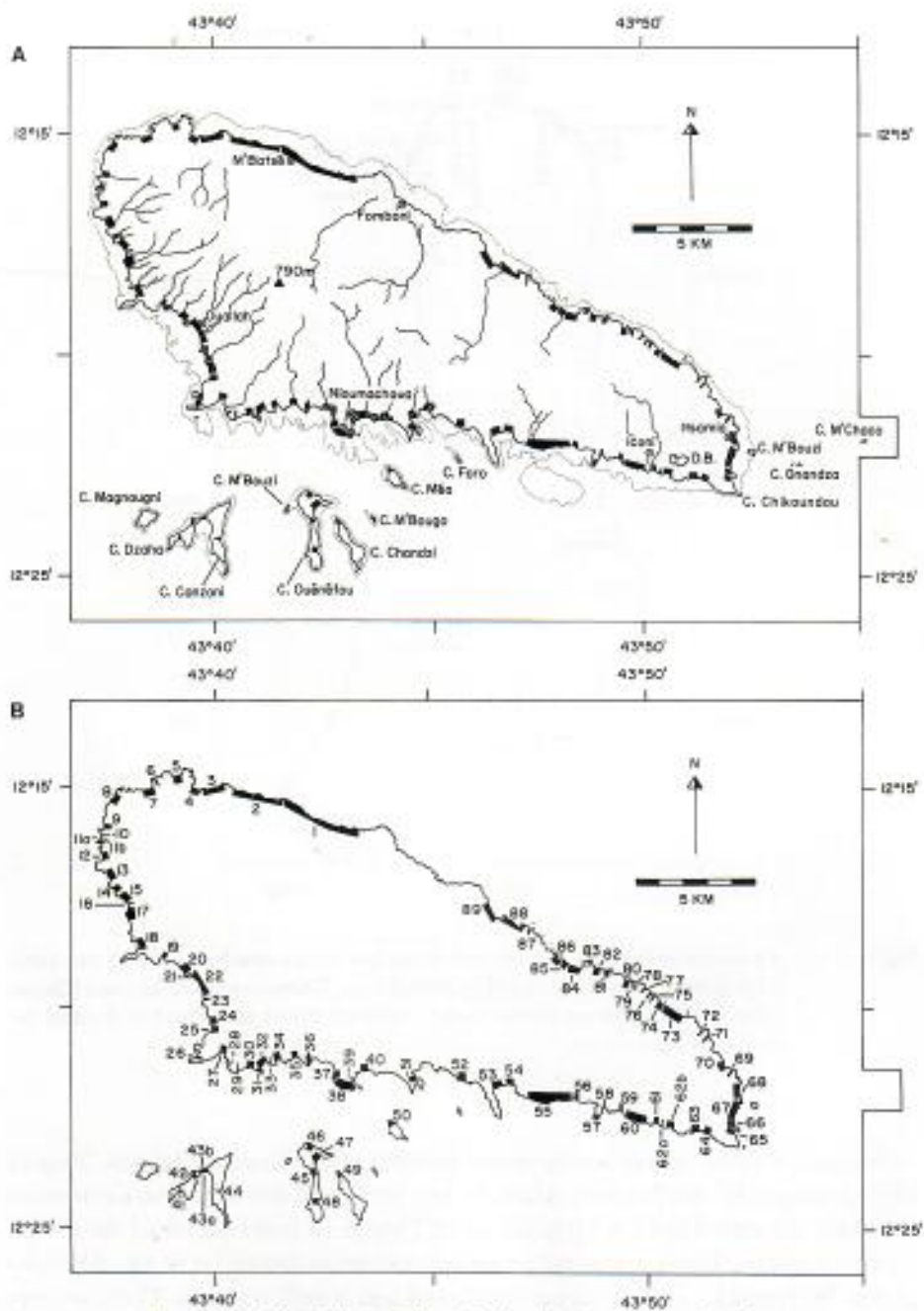
Figure 3   The island of Mohéli (see Table 2 for details). A – Geographic features: permanent
            streams and high points are shown; reefs are indicated by dotted lines, mangrove
            woods by hatched areas; Dziani Boundouni crater lake (D.B.) is shown in the
            southeast; thirteen major offshore islands are labeled; towns mentioned in the text
            are shown by open circles. B – Individual beaches are numbered 1 to 89.

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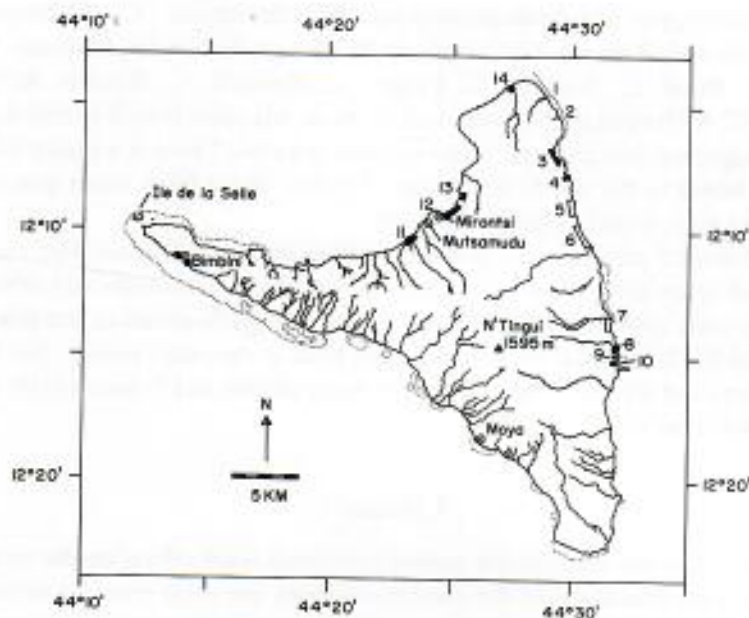
Figure 4   The island of Anjouan; individual beaches are numbered 1 to 14 (see Table 3 for details); permanent streams are shown; reefs are indicated by dashed lines, mangrove woods by hatched areas (near Bimbini); towns mentioned in the text are shown by open circles.

nearly a dozen offshore rocks, but only one significant island. Ile de la Selle, off the western point, is about 0.3 km², and 101 m high.

Mayotte is the eastern-most island of the Comoro Archipelago and the oldest of the four islands (Esson et al.,1970) (Figure 1). Bénara, the highest point, rises to 660 m in the centre of the island, and there are two other peaks, each above 570 m, in the north and south, but generally the terrain is low and rolling. The main island is about 38 km north-south by 20 km east-west; its outline is an undulating complex of bays, peninsulas and headlands (Figure 5A). Some of the bays, such as Moya on Pamanzi Island, are clearly old crater walls, but most of the volcanic rock has decomposed.

The main island is ringed almost entirely by a barrier reef that lies from 2 to 10 km from the shore. In the northeast the barrier reef is nearly 2 km wide. Several sand cays rise from the southeastern and western reefs, and there are half a dozen deep passes in the reef, mainly in the east and north.

Fringing reefs line most of the mainland shore. Between the barrier reef and the main island is a massive lagoon that is dotted with a dozen islands and many patch reefs. Circling Mayotte clockwise starting in the northwest, the major offshore islands (excluding cays and small rocks) include: Chissioi M'Zamboro,

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Malandzamiayajou, Malandzamiayatsini, C. Andréma, C. M'Songoma, Gombé-Doumé, Zissioua Ziné, Zissioua M'Tsanga, Dzaoudzi, Pamanzi, Sisoa Bouzi, C. Boué, C. Pouhou, C. Pingoi, C. Bandélé, C. Bambo, M'Sanga Tsoholé, C. M'Bouini, C. Caroni, and C. Sada. Mayotte is well watered, with many temporary and perhaps 20 permanent streams. There is a crater lake on Pamanzi Island in the northeast, 'Dziani Dzaha,' and a fresh water pan in the west of the main island, 'Dziani Caréhani.'

Small forested areas remain, but most of the land is cultivated. Hill rice and other food crops are grown over much of the Island. Coconuts and other export crops such as ylang-ylang and coffee occupy significant areas, but there appears to be less land under these plantations than at the other islands. See Saint-Ours (1957) and Benson (1960: 5 ff.) for more details and France (1958; 1959) for detailed relief maps.

Climate

Islands of this size and altitude induce numerous local effects on the weather. However, generalisations of the coastal situation, are most relevant to this report.

There are three main seasons. 'Kousi,' the Southeast Trades, blow from April to September. 'Niobene,' northerly or variable winds, last through September and November. 'Kaskazi,' or northerly winds, blow from December to March. The Southeast Trades, as is usual, are constant and fairly strong, about 16 km/h. The Comores are not usually on the direct paths of cyclones, but they are commonly subject to the side effects of storms that pass into the northern Mozambique Channel.

Air temperatures are tremendously variable, depending on altitude. Frosts may occur on the top of Kartala, but at sea level temperatures are equable, and there is little diurnal variation. The season of Southeast Trades is coolest, namely May to August.

Rainfall, like temperature, varies tremendously according to altitude. The average annual fall for 25 years at Moroni, Grande Comore, was 2,627 mm. From 1952 to 1957 annual precipitation at Fomboni, Mohéli, varied from 730 to 1,459 mm, while at Nioumachoua, on the southern side of the same island, it varied from 867 to 1,242 mm between 1951 and 1957. The 15 year average at Mutsamudu, Anjouan, was 1,899 mm. Rainfall records at Dzaoudzi indicate

Figure 5   The island of Mayotte (see Table 4 for details). A – Geographic features: permanent streams and high points are indicated, reefs are shown by dashed lines, mangrove forests by hatched areas, and major offshore islands are labeled. B – Individual beaches which were inspected are nubmered 1 to 127, those which were not inspected are indicated by letters.

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5A

Chissioi M'Zamboro

Malandzamisyajou

M'Songa Tsolé

Malandzamisyatsini

Chissioi Andréma

C. M'Songoma

Gombé-Doumé

Z. Ziné

Dzieni-Dzaha

Pomoni

Dzoudzi

Dzieni Corahani

Silépa Bouzi

Chissioi Poapoa

Chissioi Bandélé

Chissioi Corani

Chissioi Bamibo

M'Songa Tsahale

5 Km

12°35'

12°40'

12°45'

12°50'

12°55'

13°

45°   45°6'   45°10'   45°15'   45°19'

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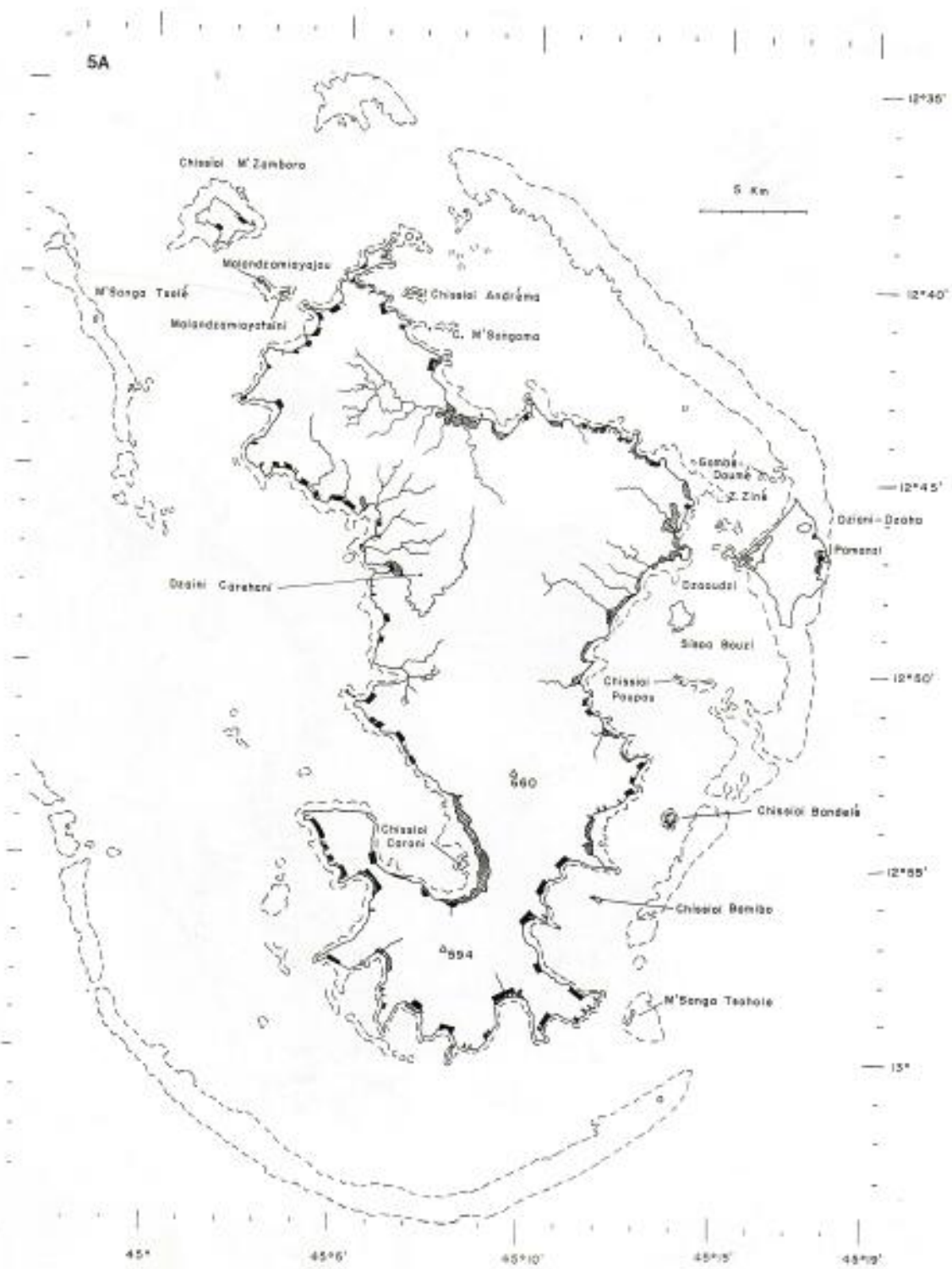
that Mayotte is drier than other islands; the annual average from 1931 to 1955 at this coastal station was 1,094 mm. All of these stations are coastal, just above sea le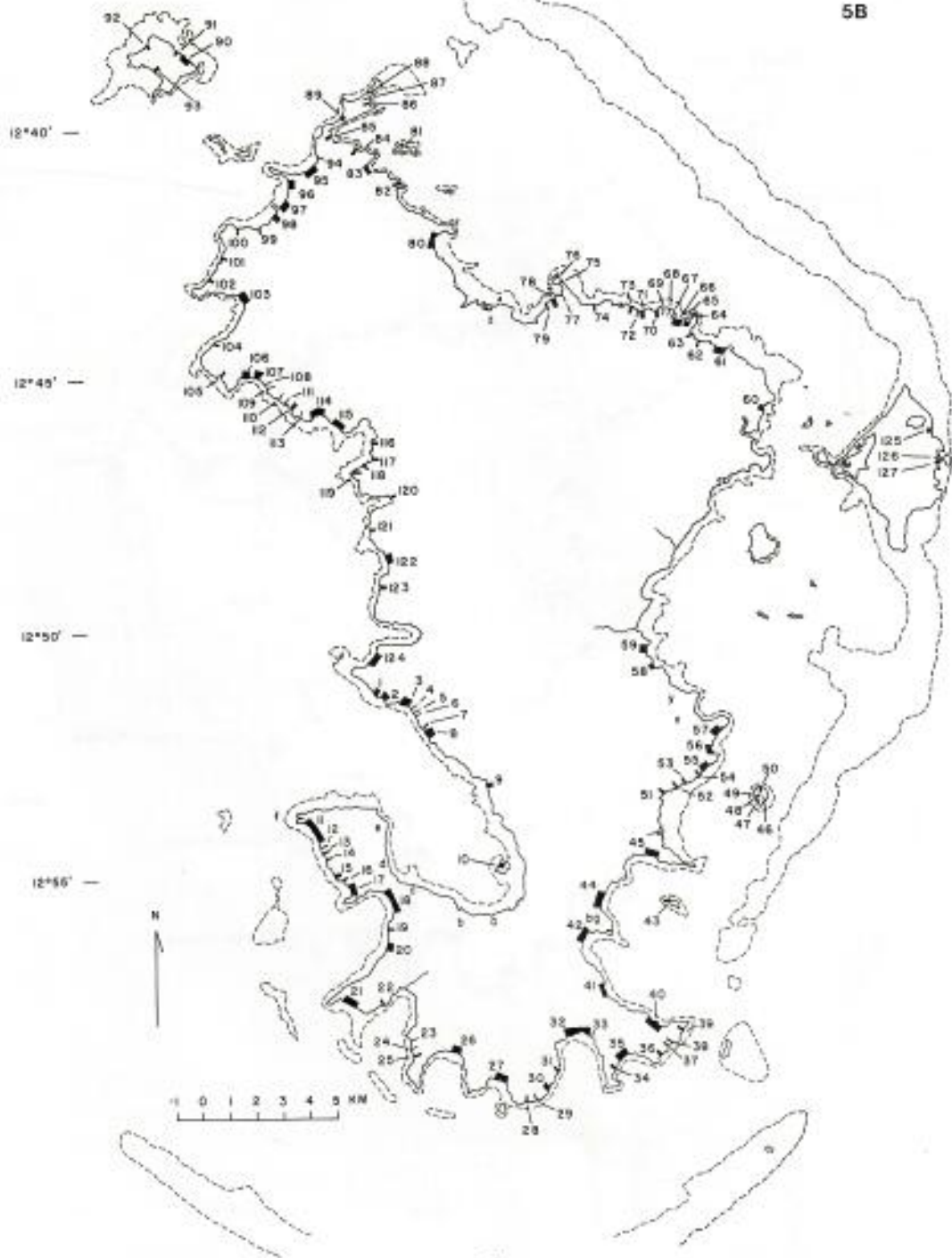vel. On the western slopes of Kartala, the annual total rainfall has reached nearly 8,000 mm. The main rainfall in Comores is from November to April (Benson, 1960: 10, 11).

Oceanography

The South Equatorial Current sweeps by the Comores all year long, but in the Southeast Trades it may reach speeds of 4 knots (= 7.4 km/hr). The main current branches and sends streams south down the Mozambique Channel, both east and west of Comores, first on clearing the northern-most point of Madagascar, and second on meeting the African mainland. There are also north-south components in this main east to west stream, and sometimes they reach greater speeds than the 'main' stream (Knauss and Taft, 1963). A drift bottle released on Aldabra was recovered on Mohéli, a straight line distance of 835 km at nearly 225° (Frazier, in prep.). Mayotte, being east and south of the other islands in the Archipelago, is probably more affected by the south-bound branch of the Equatorial Current than the west-bound branch.

With data from four stations south and east of Comores, Knauss and Taft (1963) concluded that: the main stream reaches its highest speeds at its western end (i.e., approaching the Comores), and also the pressure gradient is greater in the west than in the east – opposite to the situation in other equatorial oceans. They found no evidence of upwelling, spreading of thermo-cline, or vertical mixing, but there must be some local mixing or upwelling effects at the Comores, as the stream collides with the islands. Knauss and Taft (1964) also pointed out that there is no Equatorial Undercurrent in the western part of this ocean.

Hydrographic details of the Mozambique Channel in October and November 1957 are given by Menache (1963). Briefly, he reported that the northern sector had a surface temperature of 29° C and salinity of 35.20 ppt. McGill (1973: 64) reported an average surface temperature of 25° during the period May-June-July, and he summarised other oceanographic work. However, there are relatively few studies from the immediate vicinity of the Comoro Archipelago (see Düing, 1970; Zeitzschel, 1973).

Flora and Fauna

The flora is described in Humbert (1936 – present), and Benson (1960) also gave a valuable summary of the vegetation; quoting from Gachet's (1957) unpublished and partially classified forestry report, he listed the major areas of forest. There were less than 250 km² of forest two decades ago, and now there

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must be less. This represents less than 16% of the total land area, some of which is unsuitable for forest (e.g., the lava flows of Grande Comore).

On Mayotte, for example, Benson (1960: 16) reported 'a few tattered relics of primary evergreen forest left'. Evidently, most of the vegetation was cleared for sugar, which is no longer commercially grown, so there is a considerable area of secondary forest. The flora lacks elements of the high altitude mist forest found on the other, steeper islands. Mayotte's many protected bays harbour large mangrove woods. The largest of these, in the Baie de Bouéni, stretches over 6 km of shore line and is more than 1/2 km deep in places. There are small and scattered mangrove woods on Mohéli.

Some beaches are colonized by typical strand plants, pan-tropical or Indo-Pacific in distribution, while others are backed by dense forests and have little if any strand vegetation. In general it is the first vegetation type which occurs on beaches most important to nesting turtles.

The fauna is not well studied, with the exception of the birds. Benson (1960; 1961) treated the avifauna of the Archipelago in detail, and Forbes-Watson (1969) added further information. Blanc (1971) discussed the reptiles, and Tattersall (1977) reported on the lemurs. Milne-Edwards and Oustalet (1888) described both mammals and birds.

The marine biota is also poorly studied. Fourmanoir (1956) investigated fishes, and Polunin (1974), Crown of Thorns Starfish, *Acanthaster planci* (L). Guilcher et al. (1965) studied the coral reefs at Mayotte, and an excellent description of the marine environment of this island is given by Hentig (1973).

Most renowned of all the Comorian animals is the Coelacanth, *Latimeria chalumnae* Smith, (Smith, 1957). Recent international expeditions to Comores have specialized on this so-called 'living fossil.' A general account of both marine and terrestrial fauna is in Prosperi (1957).

Political Status

The early political history of Comores is complex. At one stage Anjouan was the seat of the Sultan and controlled Mohéli. Fighting and factions among the islands, and particularly between the islands and the Sakalava of northwestern Madagascar, lead to Mayotte's appealing to France for protection. Grande Comore, Anjouan and Mohéli all came under French protection in 1886, and they became a colony in 1912. The entire Archipelago was administered as a dependency of Madagascar from 1914 to 1946, and it attained separate status in 1947 (Guy, 1954: 6).

A unilateral declaration of independence (UDI) was made on June 6, 1975, creating the Federal and Islamic Republic of Comores. As before independence, the capital is Moroni, on Grande Comore. During UDI there was disagreement over the status of Mayotte, which has always had closer ties with

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France, and a referendum determined that it would remain with France, as a Département d'Outre Mer; its capital is on the island of Dzaoudzi.

Historical Summary

Comores were probably inhabited by Arabs no later than the 11th Century. Bantu slaves from eastern Africa were brought over and much of the present-day population stems from these ancestors. Sakalava raiders from northwestern Madagascar sailed to Mozambique, but also ravaged Comores, especially Mayotte, on numerous occasions. This was one of the major factors in Mayotte's appealing to France for protection and the consequent establishment of the islands as a French colony.

Until independence in 1975, land was owned primarily by French plantation concerns, and the economy was based mainly on the export of copra, essences for perfume manufacture (ylang-ylang especially), and spices (mostly vanilla and cloves). The more accessible lowland areas were usually under export crops while the steeper mountain slopes were subjected to slash and burn cultivation by the subsistence farmers. French plantations were smaller on Mayotte than on the other islands.

A population census in 1966 yielded estimates of 124,210 for Grande Comore, 10,845 for Mohéli and 91,650 for Anjouan (France, 1966). The calculated human densities per km^2 were thus: 131 – Grande Comore, 50 – Mohéli, and 242 – Anjouan. The population has grown, probably between 3 and 5% per annum, in the last decade, and clearly the Comores are one of the most densely inhabited areas in the western Indian Ocean. Hence, it is of little surprise that emigration has been considerable, and there are sizeable enclaves, virtually colonies, of Comorians in Madagascar and East Africa (Guy, 1954: 5; Thompson & Adloff, 1965: 270). Useful accounts of the history are in Bulpin (1958); Faurec (1961); Manicacci (1939); Toussaint (1966); and Vienne (1900).

Ethnographic Features

At present, there is little evidence of a sophisticated 'turtle culture' in the Comores. However, Petit (1930: 233) described the use of remora sucker fish at Moroni to catch turtles. This involves a complicated procedure and a highly developed technique, which indicates that at one time there was a turtle culture. On Mayotte many people are excellent sailors, and they have more sea-worthy vessels than on the other islands. However, most of the natives are subsistence farmers, who fish only secondarily.

With the exception of the Creole and French expatriates, who were relatively few in number before independence and are even fewer now, the population is Moslem. Hence, there are food restrictions, but these are not standard over

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the islands. Some people claim that turtles (and other sea foods, except fish) are unclean and cannot be eaten; some even go so far as to say that turtles, just as dogs, cannot be touched (but this is most likely to be from personal superstition rather than strict religious doctrine). Other followers of Islam eat turtle readily. Those of Malagasy ancestry have few food restrictions and tend to be less inhibited than other Comorians. On Mohéli it is said that immigrants from Anjouan eat turtles and those from Grande Comore do not; although there are exceptions, this is a reasonable generalisation. A major part of the population of Mayotte has a Malagassy ancestry and this gives the people a temperament different from that in the rest of the Archipelago; although they are Moslems, the interpretation of the Faith is not as strict, and there is little fear of eating turtles.

Chelonia mydas is eaten by many Comorians, but *Eretmochelys imbricata* is generally regarded as poisonous, or at least said to cause 'bouton' (pimples or boils) or white patches in the skin. These claims may refer to allergic reactions, or they may be merely superstitions. However, *Eretmochelys* meat is rejected as poisonous in many areas in the western Indian Ocean, but not all turtles of this species are poisonous, for some people do eat them without problems. Two young men on Mayotte claimed that some people prefer the meat of *Eretmochelys* – this is the only place in the Western Indian Ocean where I have heard of this preference. The problem of toxicity needs further study, but on the whole this turtle is not eaten in Comores.

'M'Rouhie' is a rare type of turtle reputed to be so poisonous that even touching it can be fatal. Crows that fed from the carcass of this turtle evidently died, and from this its toxic properties were probably assumed. The animal in question is thought to be *Dermochelys coriacea* (L.), which is occasionally poisonous (see Section on Unidentified Species).

Knowledge or legends of these toxic properties have doubtless contributed to the belief that turtles are unclean. It is probably those people who are least familiar with turtles that are most reluctant to touch or eat them.

The vast majority of the people are subsistence farmers and labourers on plantations. High human densities make food a problem and animal proteins are not readily available – even in fishing villages. The Comorians fish most coastal areas intensely, but they are generally not a seafaring people (except those of Malagasy heritage on Mayotte). Their knowledge of turtles is poor and capture methods are limited essentially to encountering nesting females. Detailed accounts of sociology and ethnography are in Gevrey (1870), Robineau (1966) and Vienne (1900).

Summary of the Fishery

There is no large commercial fishery in Comores, indeed the extant fishery is insufficient to feed the local population. Despite the density of coastal popu-

lations and commonness of local boats on Mayotte, fish is always in short supply, and most fish is caught for consumption by the family and friends. The demersal fishery is extremely limited, except at Mayotte, because there is so little shallow water. Hand line fishing is common from outrigger canoes; netting is less common, and spearguns have been used almost exclusively by non-Comorians. Traditional poisons are used widely in small intertidal pools. In general, exploitation is intense and the fish populations show this in smaller numbers or mean sizes and greater flight distances from swimmers than would otherwise be expected. There is a small, seasonal, pelagic, nearshore fishery, notably off the north end of Anjouan, and off the south of Mohéli.

Fish are sold where the boats are beached and rarely in markets. On the southern islands off Mohéli, men have seasonal fishing expeditions where the catch is sun-dried for later consumption, or sale. Mohéli seems to have the most fish per capita, but the catch is still insufficient.

Comores are not known as turtle islands, and Fourmanoir (1956) did not mention turtles in his review of the fishery. Yet, Parsons (1962: 51) stated that substantial numbers of *Chelonia* nested here but were much reduced; it is not clear how he obtained this information. Likewise, in his review of *Eretmochelys*, Parsons (1972: 52) mentioned that Comores, along with Madagascar and Nosi By (= Nosy Bé), exported tortoise-shell, implying that their contribution was significant, but no further information was given.

Chelonia are taken for personal consumption, and on Mayotte they are infrequently marketed. There is a small and irregular trade in *Eretmochelys* scutes. If there has been an organized turtle fishery of significance in Comores, it has almost certainly been for tortoise-shell, and probably it has been of short duration.

Research History

As indicated above, there has been little biological research in Comores, but Benson (1960: 6-8) provided a useful summary of pastwork. There has been only one study of marine turtles in the Comoro Archipelago; this consisted of two periods: three months between 5 January an 7 July 1972 and a month from 21 May to 23 June 1973 (Frazier, 1972; 1975: 171 ff.; 1977).

FEEDING HABITATS

There is a paucity of shallow water in Comores. Grande Comore is particularly lacking, for its marine slopes drop virtually to the sea bed within a few km

of the shore (Figure 2). There are small fringing reefs in the north, northeast, southeast and west, but they cover little more than 60 km of coast, and the majority of these reefs is very depauperate, or even barren, without great variety in life or texture. Sea grass pastures are limited to the northeast, near Choua-Chandroudé, but there seems to be far less than one km².

Mohéli is relatively well endowed with shallow water, particularly in the south, where deep waters may begin more than ten km from the Island (Figure 3A). Fringing reefs encircle the Island, but the most diverse reefs are in the south, notably around the offshore islands. The main marine pastures are also in the south, at Ouallah, Nioumachoua, Iconi and Itsamia, but in total there are probably not more than 5 km².

Anjouan shelves even more steeply than does Grande Comore (Figure 4). There are small fringing reefs on the east coast and in the southwest, but they cover less than 55 km of coast, and generally are not rich. The western point, at Bimbini, evidently has a very complex fringing reef. There seem to be no marine pastures of any consequence.

Mayotte's barrier reef provides a large area of protected water and complicated live reefs (Figure 5). Marine pastures are common both within the lagoon and on the outer edge of the barrier reef. Large pastures of *Thalassodendron ciliatum* (Forsk.) den Hartog were conspicuous in the southwest and northeast close to shore, and at Moya on the outside of the island there is a large pasture in shallow water. *Chelonia* were seen near or over pastures in the northeast, both inside and outside the lagoon, and inside the lagoon in the south and southwest; the animals sighted, except those off Moya, were apparently grazing. Stranded mounds of *Thalassodendron* leaves were present on the northeast shore of the Baie de Bouéni, but in general these were not abundant. The total area of marine pasture at Mayotte may be about 100 km².

The reefs of Mayotte are outstanding and provide a large and varied surface. Barrier, patch and fringing reefs all provide excellent potential feeding habitat for *Eretmochelys*. These turtles were seen in the southeast, southwest, and west over or near reefs.

In general, although Mohéli offers good marine pastures and diverse reefs, and Anjouan evidently has rich (but restricted) reefs, there seems to be little feeding habitat for either *Chelonia* or *Eretmochelys*; Mayotte, however, provides large areas of feeding habitat. The Archipelago appears totally unsuited for *Lepidochelys*, for there are no significant areas characterised by: major fresh water effluent and low salinity, high turbidity, soft bottoms and concentrated populations of prawns (cf. Hughes, 1972: 131). Neritic habitats for *Caretta* would seem to be very limited in area and poor in quality; the molluscs known to constitute a major part of the food of this turtle (cf. Hughes, 1974b: 17) are not known to occur in the Comores in great numbers. Nothing is known of the occurrence or availability of pelagic foods that might be eaten by *Dermochelys* in

the waters around the Comores [see Brongersma (1969) for a detailed discussion of stomach contents of this turtle].

NESTING HABITATS

The coast of Grande Comore is rugged. Along most of its length lava cliffs stand 3 m or more above the sea, and depending on the wind, the surf pounds full force against them. Pocket beaches are common along many stretches of shore, but the vast majority are false beaches, completely covered at high tide (Plates I and II).

There are only 43 beaches on the island, and half of these are short, 100 m or less (Table 1, Figure 2). Almost all beaches are in the north and northeast, but there are several in the southeast. There are evidently only three beaches on the entire west coast. All together the beaches total roughly 10 km. Thirteen beaches, that make up nearly half the total beach length, were examined. Much of the east coast, from Hantsindzi to Ourovéni, was not seen.

The majority of the beaches examined had white coralline sand, reflecting the recent age of the lava; all had strand-line vegetation, characteristic of the Indo-Pacific Region. Very few beaches did not have some form of regular human disturbance. Turtle spoor was seen on only one beach, but reported on three others. More nests were possible on most of the beaches that were examined, but the large human population and intense interference must preclude many turtles from nesting on Grande Comore.

Mohéli's coast has been tempered by time and the sea. It does have frequent cliffs, but they are much less dominant and far less rugged than on Grande Comore. Instead, the island (with its offshore satellites) is generously provided with at least 92 beaches. Eighty-nine beaches were examined, 84 in detail (Table 2; Figure 3B). Mombasa and M'Batsé in the north-west of the Island are the longest beaches, 2 and more than 3 km in length, respectively. There are also many beaches of less than 100 m in length. Beaches are found right round the Island, and also on the offshore islands to the south (Plates III through VI: Figure 1). The total length of beach at Mohéli is 26.3 km. Thirty-six, or 40%, of the beaches, totalling 6.565 km, had turtle nest spoor, and these made up 25% of the total beach length. The eight longest beaches on the Island (800 m or more) made up nearly 40% of the total beach length; all but one were next to villages and certainly turtles would be discouraged from nesting there by disturbance or predation.

White calcareous sand is characteristic of the offshore islands in the south,

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while brown, grey and pink terrestrial sands are found on the main island beaches. Almost all beaches are vegetated with typical strand vegetation, and many also have terrestrial scrub forests immediately inland of the strand zone. Mangroves are present at 11 of the beaches, and actually dominate several. Coconut plantations extend right down to the beach in at least 17 localities.

The beaches with the most nesting activity are mainly in the extreme eastern and western ends of the Island, along with those on offshore islands in the south. There is no obvious characteristic that is common to these important nesting beaches other than being relatively undisturbed.

Anjouan, like Grande Comore, is poor in beaches. There are only about 14 beaches, and some of these are cobble and without sand. Ten were examined, seven in detail (Table 3, Figure 4). Only the northern half of the east coast and the northwestern shore were examined. The total length of sandy beach is 6.48 km. Individual beaches range from 15 to 2,100 m long. Most, if not all, of these Anjouan beaches are of terrestrial sands. The steep contours of the Island result in narrow beaches with very limited supralittoral zones.

Ile de la Selle is without beaches as are the other smaller offshore rocks. The few beaches of Anjouan are utilized by an extremely dense human population; the result is that they are greatly disturbed by human activity. Nesting was reported from two beaches, but no first-hand evidence was seen.

At Mayotte a total of 137 beaches were recorded (Table 4, Figure 5B). About 7 km of heavily populated shoreline in the northeast of the Island and the associated islands were not examined at close range, and parts of Pamanzi Island were not checked either. Hence, about a dozen beaches have been omitted from the list. The coast had gentle slopes, and good nesting beaches were all round Mayotte and on offshore satellite islands (Plates VI: Figure 2 and Plate VII); sandy beaches ranged in length from 20 m, e.g., M'Rafeni, to more than 1 km, as at Bouéni and M' Zouazia. Of the 126 beaches whose lengths were estimated, 38% were less than 100 m; only 10% were more than 500 m. Long and short beaches were all round the island, but most of the long beaches were in the southern half. The total length of beach at Mayotte was well over 27 km.

The expanse of sand above the high water mark was narrow, never more than 15 m, and most beach widths were 5 m or less. Hence, although beaches were vegetated by typical strand species, dense forest usually occurred right up to the landward edge and often shaded much of the beach platform. Beaches inside bays are often sheltered by mangrove forests; there were at least 15 mangrove-fronted beaches. The east coast was especially fringed with these intertidal forests. Coconut plantations were behind a third of the beaches, and of all beaches examined, 37% had villages or human habitations. Only 27% had no obvious human distrubance. Sand colour varied from black, of volcanic origin, to brown, grey, pink and finally white, from marine organisms; terrestrial sands are most common.

Nineteen beaches had signs of nesting, but only half of these had more than 10 nests. Most nesting activity was recorded on the east coast of Pamanzi Island and in the southeast, near Passe Saziley Sud. Only this last named had concentrated nesting inside the barrier reef.

SPECIES ACCOUNTS

Two species, *Chelonia mydas* and *Eretmochelys imbricata*, are definitely recorded in Comores, and both nest. A third species is reported, but was never seen during the survey; it is thought to be *Dermochelys coriacea*.

Chelonia mydas (Linnaeus)

Curiously, the Comores have not been known as a Green Turtle area, but they have one of the most important breeding areas in the western Indian Ocean.

Common Names in Use

As Guy (1954: 6) points out, the various island dialects are often very different; this is especially troublesome with plant and animal names. On Grande Comore all turtles are called 'Nyamba' (Gevrey, 1870: 115, records 'Namba'), and the species are rarely differentiated. At Mohéli, species distinctions are made and three names may be applied to *Chelonia*; in order of commonness they are: 'Nyamba', 'Kasa', and 'Dusi'. On Anjouan 'Kasa' (occasionally 'Katsa') and 'Nyamba' are used. All of these names are recorded from the Swahili-speaking coast of eastern Africa, from southern Somalia through Kenya and Tanzania, to northern Mozambique. 'Dusi' is no longer used, but the other names are still in common usage.

The common names used in Mayotte are both Swahili and Malagassy in origin: 'Nyamba,' 'Kasa,' and 'Kaza' are Swahili, and 'Fanu' is Malagassy. These may be used as general names, but they are also applied specifically to *Chelonia*.

French names common throughout the region are: 'Tortue de Mer', 'Tortue Franche', 'Tortue Mangeable', and, infrequently, 'Tortue Verte'. The English name is 'Green Turtle', and less commonly 'Edible Turtle'.

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Occurrence

The species occurs and nests throughout the islands. Each of the islands will be dealt with separately as their respective populations are thought to be separate (See Section on Movements and Migrations). At Grande Comore *Chelonia* was seen in the northwest, west and northeast, notably all areas where a significant amount of time was spent; other parts of the Island were not well surveyed. Records date from May to September. The species presumably occurs right round the Island and throughout the year. At Mohéli it is recorded on all sides of the Island, with important breeding concentrations in the east, south and west (Tables 2 & 5). *Chelonia* was documented from February to June, and doubtless occurs the year round. I have no firsthand records from Anjouan, but *Chelonia* is reported from the northwest and the southwest and in the month of June. Probably it occurs round the Island and throughout the year. *Chelonia* is clearly less common at the steeply shelving and densely populated islands of Grande Comore and Anjouan than at Mohéli.

On Mayotte *Chelonia* were seen in the northeast, inside and outside the lagoon, and in the southeast and southwest. Nesting spoor from this species was in these areas and also in the west. A total of 17 beaches had large nests and tracks typical of *Chelonia*, and in nine cases the remains of this species were confirmed on the beach. One other beach had bones of *Chelonia* but no nest spoor (Table 4). There was no direct evidence of these turtles in the north of Mayotte. They are thought to occur all around Mayotte and to be more abundant near marine pastures.

Chelonia and fresh nesting spoor were seen from the 7th of April until 18 June. A nesting female with two sizes of enlarged follicles on 8 June indicated subsequent nestings would have been made at the end of June and in mid-July. This species probably occurs in the protected lagoons at Mayotte throughout the year – possibly there is even a small resident population.

Population Size and Structure

Grand Comore. At the largest island immatures were occasionally captured, and they are said to be commonly netted in the Mitsamiouli area. An animal caught in a net (JFCm 787) measured 40.5 cm curved carapace length (Table 6) and was thought to be representative of the size usually taken there. Perhaps a dozen or so animals of about this size are landed in a year in this area. Immatures doubtless occur and are caught in other localities at Grande Comore, but there are no records. They may well occur throughout the year, but there are no documented dates. The immature population at Grande Comore seems to be small – probably a few hundred.

An adult male (JFCm 862) was found dead opposite Choua-Chandroudé in

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the northeast (Table 6). Males were also seen while SCUBA diving off the reefs at Bangoi-Kouni (in the north) and Iconi (in the west) on 24 and 28 May 1973, respectively. No further information is available on the adult male population at Grande Comore, but it would appear to be small, probably not more than a few hundred. Considering the situation at Mohéli (see below), the adult male population is likely to occur seasonally.

No females were handled or even seen at Grande Comore. Nesting was reported by Mr. Pichard at Chindini (in the southeast), and both a nesting and hatchling emergence were reported by Mr. Chevalier from Mitsamiouli (in the northwest), from January and September respectively. Only one record of a nest pit was recorded anywhere in Grande Comore: on the beach south of Choua-Chandroudé (in the northeast) (Table 1). The species seems to nest in several localities, both north and south, but always infrequently. The annual nesting population is unlikely to be more than a dozen animals, and it is likely to occur seasonally.

Mohéli. *Chelonia* were particularly common at Mohéli. Numerous sightings were made in the south, near marine pastures and nesting beaches around the offshore islands (Table 5). One animal, sighted 29 March 1972, was clearly immature. An immature (JFCm 785) was caught by a fisherman at Fomboni on 23 March 1972. Animals of this size are suspected to occur round the Island and throughout the year, but the available information is insufficient to prove this. It is not known how large the immature population is, but Mohéli is more likely to support a population than is Grande Comore, and there are better chances for animals to be resident with the larger areas of shallow water, reefs and marine pastures.

One animal (JFCm 797), thought to be a male, was handled at Mohéli (Table 6). Males in copulation were seen off all the major nesting beaches (except N° 8); and escorts, or accessory males, were frequently recorded near the coupled pairs (Table 5). The preponderance of records from the offshore islands in the south is, at least partly, a bias caused by the great amount of observation time spent in a small boat among the islands. Nevertheless, it is possible that there is actually a concentration of males around the islands, for there are several important nesting beaches here, and copulation is commonly seen off of nesting beaches.

It is notable that no observations of males in copulation were made in June 1972 or June 1973, although nesting activity was intense in these months. The absence of observations of turtles in copula, when large numbers of females are present, indicates that mating behaviour is seasonal (see Booth & Peters, 1972: 809). This may also be taken as evidence that the male population is seasonal in occurrence. There is, however, no way to estimate the size of the male population. The concentrated predation on nesting females (see Section on Human Predation) may result in a preponderance of males. But, the fact that as many

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as six escorts may gather at a breeding pair is no proof of a disparate sex ratio. Such concentrations in courting males are documented from a remote population in Australia where females actually outnumbered males (Booth & Peters, 1972: 808).

Twenty-five nesting females were handled, and 34 specimens that had been killed on nesting beaches were handled (Tables 7 and 8). Many of the slaughtered specimens were clearly female, and since the chances of capturing a male on a beach are very small, all specimens are assumed to be female. Furthermore, these two groups are assumed to be mutually exclusive, although there is a chance that a female handled while nesting could have been slaughtered at a later date, even on another beach. Sightings of animals in copulation are reported in Table 5.

The annual female nesting population for Mohéli was estimated from censuses of activity on nesting beaches. Of the 84 beaches that were examined in detail, 30, distributed all around the Island, had clear signs of *Chelonia* nesting. There were questionable signs of *Chelonia* nesting on 3 other beaches, and two others had reports of incidental nesting. Although five other beaches had *Chelonia* bones or slaughters (evidently a male on N° 22), they had no signs of nesting (Table 9). Twenty-four beaches had low nesting activity by *C. mydas*, each estimated to have less than 150 nests annually; three others had low nesting activity, possibly by *C. mydas*, and two had reports of nesting but no direct observation. Six beaches had high nesting activity, each with 450 or more estimated nests per year.

The nesting beaches of lesser importance will be discussed first. These beaches were surveyed once each; four exceptions were each surveyed on two or three different occasions: Sambadjou (N° 24), Tsinavouni (N° 65), no name (N° 66) and Itsamia (N° 68). Beaches 65 and 68 had significant amounts of nesting and were probably used by some of the same females nesting on the nearby and heavily used M'Sanga Nyamba beach (N° 67).

For each beach that was visited once only, the beach platform was checked for nesting spoor, and a tally was made of the nests estimated to have eggs and those without eggs; a third category included nests of uncertain status. The details of this procedure are described in Frazier (1975: 164 ff.).

Because none of these minor beaches had crowded nest pits, it was assumed that the spoor tallied represented roughly a three-month period. It was further assumed that the nesting activity during the period surveyed was representative of an average three-month period in the year. Hence, the annual total was estimated as 4 times the number of nest pits with eggs. If the number uncertain to have eggs was large, it was added to the number of nests with eggs before calculation of the annual estimate. It was further assumed that on average a female nests three times a season, and the annual estimate was rounded to a multiple of three to facilitate calculation of the annual number of females nesting. These

estimates were modified depending on the condition of the beach, particularly the presence of turtle bones and remains, and the state of beach vegetation. It must be emphasized that the values calculated serve only to estimate an order of magnitude, and should be used as only rough 'population estimates'; there simply is insuffucuent data to provide a greater degree of precision.

The four minor beaches surveyed repetitively showed seasonal increases, as did the six major nesting beaches (see Appendix 1). In these cases figures from the second survey, the time of most activity, were used in the calculation. This raises questions about the assumptions made in estimating, but unfortunately, the data are limited to these imprecise procedures.

In total there were estimated to be more than 1,000 nests annually on 27 beaches with low *Chelonia* nesting activity. Estimates for the six major nesting beaches were derived individually for each beach (see Appendix 1). The total estimate for major beaches was 4,500 nests for the year 1972. Spot checks on all but the most important beach in 1973 showed that there had been some increases and some decreases compared with the same month of the preceding year, but on the whole the numbers nesting did not seem to be greatly altered.

The total for all beaches on Mohéli was 5,550 nests annually. To estimate the annual number of females nesting it was assumed that on average a female nests three times a season. In fact, many populations have females that are thought to nest at *least* this often (Hendrickson, 1958: 499 ff.; Hirth, 1971: 3: 4; Schulz, 1975: 71), and there is evidence that the Mohéli population is similar (see Section on Breeding Biology). Hence, the population estimate should be a conservative maximum. The estimated annual nesting population at Mohéli is 1,850, or in the order of 2,000.

Anjouan. The situation at this island seems similar to that at Grande Comore. No *Chelonia* were seen here. Mr. Chevalier showed me the carapace of a sub-adult that he shot (with speargun) at Mirontsi, in the north (JFCm 786; Table 6). There is doubtless a small population of immatures at Anjouan.

No adult males were seen or reported, but they probably occur off the reported nesting beach at Moya. The population must be small.

No signs of nesting were seen anywhere along the east coast from Banda M'Tsanga in the north to Bambao halfway down the coast. However, both Comorians and French alike reported nesting on Moya beach, in the southwest. Mr. Chevalier also reported a beaching of a gravid female on Mirontsi beach in the north; this animal's carapace was examined (JFCm 863; Table 6).

The lack of information makes it difficult to estimate population size, but it seems unlikely that there would be more than a few dozen animals nesting annually on Anjouan.

Mayotte. Immature *Chelonia* were seen in the northeast and in the south of Mayotte. They were said to be common in the lagoon. Possibly they are resident at this island, for there is a considerable area of sheltered water.

Male *Chelonia* were seen off of both Saziley and Moya, important nesting areas. They were seen nearly every time I went skin diving at Moya, and although some turtles would flee, many would appear, as if by magic, and show considerable interest in me. The competition for females is evidently intense; five males were seen milling about a single female. However, these observations cannot be taken as evidence for an overabundance of males, for the females may not be as conspicuous (cf. Booth & Peters, 1972: 808). Since nesting females bear the brunt of human predation, one might expect that males are more numerous; however, there is no means of estimating the numbers of immature or male *Chelonia* at Mayotte with the few data available.

Seven females were tagged and released (Table 10), and 43 carcasses were examined, 37 in 1972 (Table 11) and 16 in 1973 (Table 12). All but one carcass were on Moya and Papani nesting beaches of Pamanzi Island. Most of these turtles were clearly females, with short tails and/or eggs; as the chances of catching a male are small, all of these specimens are assumed to be nesting females.

An estimate of the number of nesting females can be made, based on the survey of nesting beaches. Of the 127 beaches examined, 17 had signs of *Chelonia* nesting. Fourteen nesting beaches were visited only once, and they had less evidence of nesting than did the other three beaches that were observed over a période of two weeks. Hence, the groups will be treated separately.

None of the 14 beaches had crowded nests, so the nesting spoor observed was assumed to represent the nesting activity of three months. The calculations were the same as those described above for Mohéli. The total estimate for the 14 beaches is 275 females nesting annually (Table 13). This is considered to be a maximum.

The three beaches on Pamanzi Island were studied in greater detail. Estimates were derived by two methods: calculating changes after a two-month interval, and direct observations and counts over a two-week period. In order to estimate the yearly total, several assumptions were made: that the periods under observation were representative; that none of the females slaughtered during the observation period ever nested during the same period (i.e., that the individuals nesting are distinct from those slaughtered); and that the average female nests three times in a season.

The two Moya beaches were examined on 7 April and two months later on 10 June. The new nest pits that were made and the turtles that were slaughtered during this period were recorded. Three and six females were slaughtered, respectively at Moya North and Moya South, during this two-month period. Over the same time, six and 33 nests were made on these beaches, so the total number of females that might arrive in one year would be 30 and 102, respectively. The total annual estimate for the Moya beaches would thus be 132 (Table 14). No estimate was made for Papani beach.

All three of the Pamanzi beaches were observed from 28 May until 10 June, when I was camping at South Moya. During this two-week period, the numbers of nests and slaughtered animals were recorded (Table 15). The estimated values for one year are comparable to those from the above method, although Moya North had less slaughters and more nests, while Moya South had the converse. However, the estimates for the total numbers of females for these two beaches are almost identical. The total estimate for the three Pamanzi beaches is 287 females in a year.

The total estimate for Mayotte, 275 from minor beaches and 287 from Pamanzi beaches, is 562. Less than 600 female *Chelonia* are estimated to attempt to nest annually at Mayotte.

The number of nesting beaches that are available but unused or little used suggests that Mayotte could support considerably more nesting *Chelonia*. Beaches inside the lagoon may, however, be unacceptable to this species. The Pamanzi beaches, which are the only beaches on Mayotte that face directly onto the open ocean, are heavily used, while larger beaches facing onto the lagoon are little used. There is no way to evaluate the annual estimate, for there are no comparable data. With the intensity of present exploitation on nesting females, it is likely that the population has declined, and some local people claim that this has happened.

Comores. In total, the immature population in the Archipelago would seem to be small, some hundreds probably. However, further studies, especially at Mohéli and Mayotte, may alter this estimate.

The adult male population is likely to be larger than the adult female population, by virtue of the selective predation on nesting females (see Section on Human Predation). However, there is no way of estimating its size.

With a dozen females on Grande Comore, 1,850 on Mohéli, a few dozen on Anjouan, and less than 600 on Mayotte, there would be about 2,500 females nesting annually in the Comores.

Aside from Parson's (1962: 51) comment that the Comoro population has declined, there seems to be no information on population trends of *Chelonia* at these islands. There is every reason to suspect that the numbers have declined because of the increased human populations with their increased effects on nesting habitats and increased predation, but there is no way to document the past situation. The only relevant anecdote applies to the Sambadjou beach on Mohéli. Mr. J. C. Boyer showed me the site of an old house where a man once lived and slaughtered turtles on nearby beaches; there were not enough turtles in this section of Mohéli now to warrant his presence.

Movements and Migrations

The status of immature turtles is a mystery anywhere, and there are no data

from the Comores that will resolve this. In view of the limited areas of shallow water, it is likely that at least some of the immatures at both Grande Comore and Anjouan are migrants, or part of a mobile population that passes by the Comores, and not long term residents of these respective islands. Mohéli, which has a much greater area of shallow water and grazing habitat, may well have its own immature population. Immature *Chelonia* that occur at Mayotte could also be residents.

The movements of adult males are likewise a mystery. It is probable that at least some of the adult males that occur in Comores are migrant. At Grande Comore and Anjouan migration is even more likely, for these two islands have small areas of shallow water and provide little feeding habitat.

The situation with nesting females is little clearer. None of the 24 Mohéli females and none of the 7 Mayotte females tagged while nesting has been recaptured, in Comores or elsewhere. Considering what is known of other, better studied populations, several assumptions can be made. A female is likely to nest several times in one season on the same beach. This has been shown for both mainland and island nesting populations. Sometimes the ability to home on a particular stretch of beach is remarkable and this ability is seen both within a single season and between seasons (Carr & Carr, 1972; Carr, 1975: 552; Carr, Carr & Meylan, 1978: 35-37; Schulz, 1975: 75). Populations that nest on islands are known to be true to a 'home' island. Hendrickson (1958: 497) reported that only 215 of 5,748 records of returning females involved changes, and 125 of these were between islands less than 500 m apart. The Comoro Islands are about 50 km, one from the other, so the chances of such interchange would seem even less.

However, with the amount of human disturbance that exists in the Comores, it is likely that some females may break tradition and leave the home beach. It is known that a female disturbed while nesting may move a considerable distance from her home site (Carr, 1975: 553). In the Comores, the magnitude of these movements may involve simply swimming along the coast to a nearby beach, or even going right round the island to a distant beach. Movements between islands do not seem probable, but there is a record of an internesting movement (caused through disturbance in handling?) of 40 km between Galapagos Islands (Carr, 1975: 553).

At least a sizeable proportion of the nesting population is likely to migrate from nesting to feeding grounds; again this assumption is based on the findings of the other populations, although some western Indian Ocean populations may be relatively sedentary (Frazier, 1981). The most likely areas where Comoro turtles would feed are the west coast of Madagascar and the mainland coasts of Tanzania and Mozambique. It is entirely possible that populations feeding in two or more areas have one common rookery (Carr, 1975: 550).

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More specimens were handled at Mohéli than anywhere else in the Comoro Archipelago: 25 nesting females, of which 21 were measured (Table 7) and 34 carcasses, of which 30 were measured (Table 8). The carcasses were all on nesting beaches; about half of these were clearly females with short tails and/or eggs in the body cavity. There seems little reason to doubt that all of these carcasses were females, the chances of a male being captured on a nesting beach are so small. Consequently, Tables 7 and 8 will together be considered to represent females from the population at Mohéli in 1972.

Curved carapace lengths of nesting females range from 102.5 to 122.0 (mean $\pm$ one standard error $= 112.322 \pm 0.704$) (Figure 6). There is no significant difference between the lengths of live and dead specimens ($F_{20,29} = 1.35$, N.S. [not significant]; $t = -1.90$, d.f. $= 49$, N.S.), but the latter show a bimodal distribution. The peaks are neither an effect of season nor locality, for values falling in both peaks occur throughout the study period and in several localities. Neither the distribution of dead nor live and dead animals shows statistically significant kurtosis (dead: $g_2 = -1.376$; $t = -1.65$; total: $g_2 = -1.059$; $t = -1.61$; see Sokal & Rohlf, 1969: 112-118, 137, 171). Thus, the apparent bimodality can be given little importance; and the distribution will be assumed to be approximately normal.

Curved carapace width varies from 95 to 115 cm (103.141 ± 0.603). There are no significant differences between nesting females and slaughtered specimens ($F_{20,29} = 1.73$, N.S.; $t = 0.22$, d.f. $= 49$, N.S.), and there is no locality or season effect, but the distribution does not show one distinct mode (Figure 7).

Curved carapace width is positively related to curved carapace length (Figure 8). There is an indication that dead animals were relatively narrower, but in an analysis of covariance (see Snedecor & Cochran, 1967: 432 ff.) there are no significant differences between the regression lines for live and dead specimens:

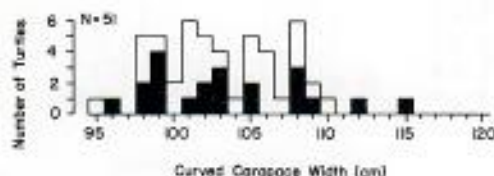|	linear equations	log log transformation
variance ratio	$F_{28,19} = 1.22$, N.S.	$= 1.25$, N.S.;
slopes	$F_{1,47} = 3.57$, N.S.	$= 3.11$, N.S.;
elevations	$F_{1,48} = 3.10$, N.S.	$= 2.95$, N.S.

Figure 7   Size-frequency distribution for curved carapace width of *Chelonia mydas* at Mohéli, Comores; sample includes 21 nesting females (black) and 30 specimens found dead on nesting beaches assumed to be nesting females (white)(see Tables 7 and 8).

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Immatures. Only three immature *Chelonia* were handled. One specimen (JFCm 787) was captured by fishermen, presumably using nets, in the Mitsamiouli area of Grande Comore, and purchased and pickled by the owner of the Hotel Maluga about September 1971 (Table 6). A second immature (JFCm 785) was captured by fishermen in the Fomboni area of Mohéli; it was purchased, measured, tagged and released. Both of these animals were just over 40 cm in curved carapace length, and at this size they would appear to be at least two years old (cf. Schmidt, 1916: 22; Frazier, 1971: Figure 4). The immature taken at Anjouan by Mr. Chevalier was over 80 cm long and clearly several years old.

Males. Only two specimens thought to have been males were handled (Table 6). One (JFCm 862) with a long tail, and thus unquestionably male, was 98.5 cm long. Compared with the much better documented, nearby, Aldabra population (Frazier, 1971: Figure 7) this animal was of adult size. A carcass (JFCm 797) found at Ouallah beach, Mohéli, was thought to be that of a male. No sign of tail or pollex claws was seen; but the carapace, relatively short and narrow, was characteristic of a male (Frazier, 1971: 387; see below). In addition, the body cavity contained a large volume of marine plants that had clearly been eaten by the turtle. Females, at least nesting animals, rarely have much food in the stomach (see also Carr, 1975: 552). In comparison with the Aldabra data, this animal is also of adult size. Evidently, the carapace of adult male *Chelonia* in Comores is smaller and relatively narrower than that of adult females, comparable to the situation on nearby Aldabra (Frazier, 1971: 387).

Females. No females from Grande Comore were handled and only one carapace from Anjouan (JFCm 863) was examined (Table 6). There is nothing remarkable about this specimen; its measurements conform with those of the large series of females from Mohéli (Tables 7 and 8). A female said to have nested at Mitsamiouli, Grande Comore in January 1972 was reputed to weigh 200 kg. While this is heavy, it is not outside the known range of weights for the species (Hughes, 1974a: Table 7). However, the weight could well have been estimated and not actually measured.
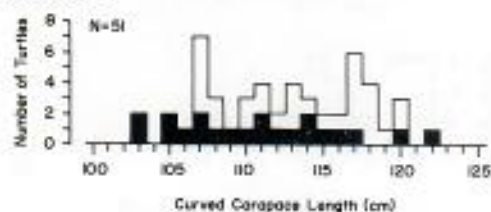

Figure 6   Size-frequency distribution for curved carapace length of *Chelonia mydas* at Mohéli, Comores; sample includes 21 nesting females (black) and 30 specimens found dead on nesting beaches assumed to be nesting females (white)(see Tables 7 and 8).
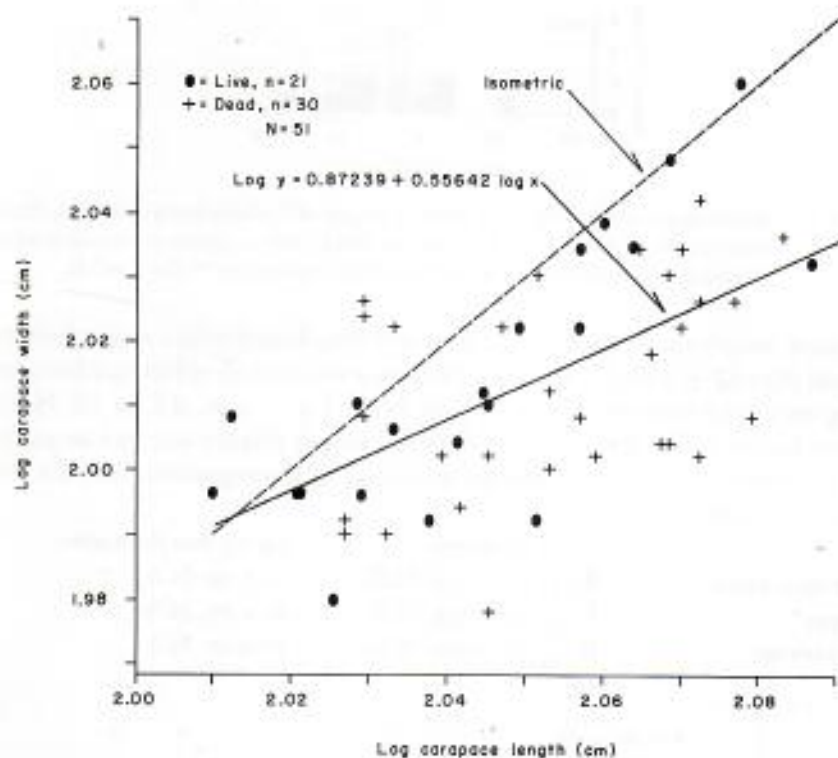
Figure 8   Relationship of log curved carapace width to log curved carapace length in female
Chelonia mydas at Mohéli, Comores, showing least squares fitted line and theoreti-
cal isometric line.

In these adult females, relative curved carapace width decreases with increas-
ing curved carapace length: the slope for the total population of log log trans-
formed data in Figure 8 is 0.55642, considerably less than 1.0, the isometric line
($t = -4.22$, d.f. $= 49$, $p < 0.001$; for comparison of two regression coeffi-
cients, see Bailey, 1964: 97–98). This indicates that the width-length relation-
ship in females is allometric (see Huxley, 1972: ix ff.)*.

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* There is apparently not unanimous agreement on the terminology. I here use 'allometry' as
Huxley (1972: ix) defined it: '*different* rates of growth of parts of the body *relative* to that of the
body as a whole' (italics mine). His use of the term 'heterogonic' (p. 8) is synonymous. 'Isometry'
is here used for the condition in which a body part changes in size at the same rate as the body
as a whole. This is synonymous with his use of the term 'isogonic'. Huxley treats isogony as a
special case of heterogony, but they are used here as mutually exclusive phenomena, which is
consistent with the roots of these words: 'allo' or 'hetero' meaning 'other' or 'different' and 'iso'
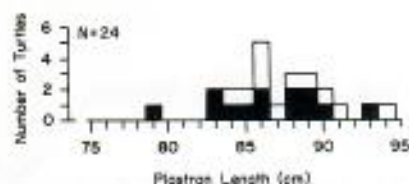meaning 'equal' or 'same'.

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Figure 9   Size-frequency distribution for plastron length of *Chelonia mydas* at Mohéli, Com-
ores; sample includes 13 nesting females (black) and 11 specimens found dead on
nesting beaches, assumed to be nesting females (white)(see Tables 7 and 8).

Plastron length measurements are normally distributed with a range from 79
to 94 cm (87.054 ± 0.689) (Figure 9). There is no significant difference between
nesting and dead animals ($F_{12,10} = 1.48$, N.S.; $t = -0.96$, d.f. $= 22$, N.S.).
Plastron length is strongly related to carapace length (Figure 10), and an analy-
sis of covariance shows no significant difference in the regression lines for live
and dead animals:

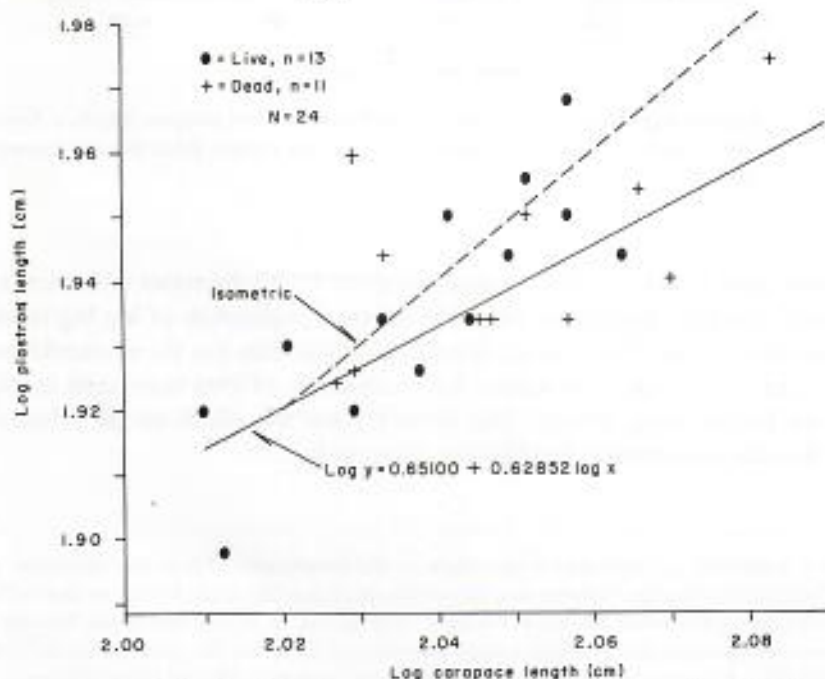|	*linear equations*	*log log transformation*
variance ratio	$F_{9,11} = 1.54$, N.S.	$= 1.49$, N.S.;
slopes	$F_{1,20} = 2.65$, N.S.	$= 2.73$, N.S.;
elevations	$F_{1,21} = -0.00$, N.S.	$= 0.01$, N.S.

Figure 10   Relationship of log plastron length to log curved carapace length in female *Che-
lonia mydas* at Mohéli, Comores, showing least squares fitted line and theoretical
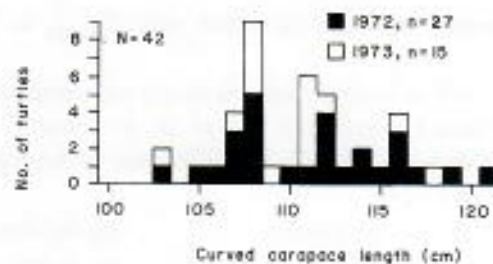isometric line.

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Relative plastron length shows the same trend as does relative carapace width: it decreases with increasing carapace length. The slope of the predictive line for log log transformed data is 0.62852, significantly less than that of the isometric line ($t = -2.92$, d.f. $= 22$, $p < 0.01$). This indicates an allometric reduction in plastron length.

At Mayotte, with few exceptions, only nesting females from beaches on Pamanzi Island were available for study (Tables 10, 11 & 12). Seven females were examined and released, and 43 carcasses were measured: 37 in 1972 and 16 in 1973. In most cases these specimens were known to be females by their short tails or the presence of eggs; as the chances of capturing a male on a nesting beach are small, all the carcasses from nesting beaches are assumed to be females.

Curved carapace length varied from 102.5 cm to 121.0 cm, averaging 110.76 ($\pm$ 0.648) (Figure 11). The major mode is at 108 cm, but there are two other modes at 111 and 116 cm. There is no significant difference between the animals from 1972 and those from 1973 ($F_{14,26} = 1.56$, N.S.; $t = 0.99$, d.f. $= 40$, N.S.). The kurtosis from the multiple modes is not statistically significant ($g_2 = -0.280$; $t = -0.39$).

Curved carapace width varies from 93.5 cm to 114.0 cm, averaging 101.50 ($\pm$ 0.724) (Figure 12). The mode is at 102 and central to the distribution. There
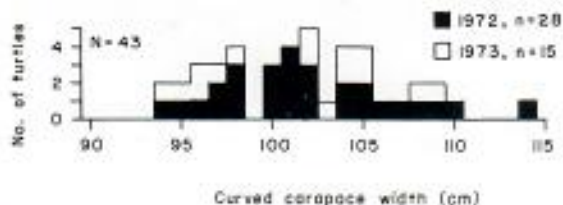
39

is no significant difference between 1972 and 1973 ($F_{14,27}$ = 1.00, N.S.; t = 0.57, d.f. = 41, N.S.).

Curved carapace width is strongly related to curved carapace length (for the log log transformed data: r = 0.69283, d.f. = 40, p < 0.001) (Figure 13). An analysis of covariance shows no significant difference in the regression lines for specimens from 1972 and 1973:

	linear equations	log log transformation
slopes	$F_{1,38}$ = 0.188, N.S.	= 0.300, N.S.;
elevations	$F_{1,39}$ = 0.000, N.S.	= -0.010, N.S.

The slope of the fitted line for the log log transformed data (0.85335) is not significantly less than 1, the isometric line (t = 1.04, d.f. = 40, p < 0.1).

Plastron length varies from 79.0 to 92.5 cm (86.281 ± 1.006) (Figure 14). The mode is central at 86.0. All 16 measurements are from 1972, so there is no way to investigate this parameter in the 1973 population.

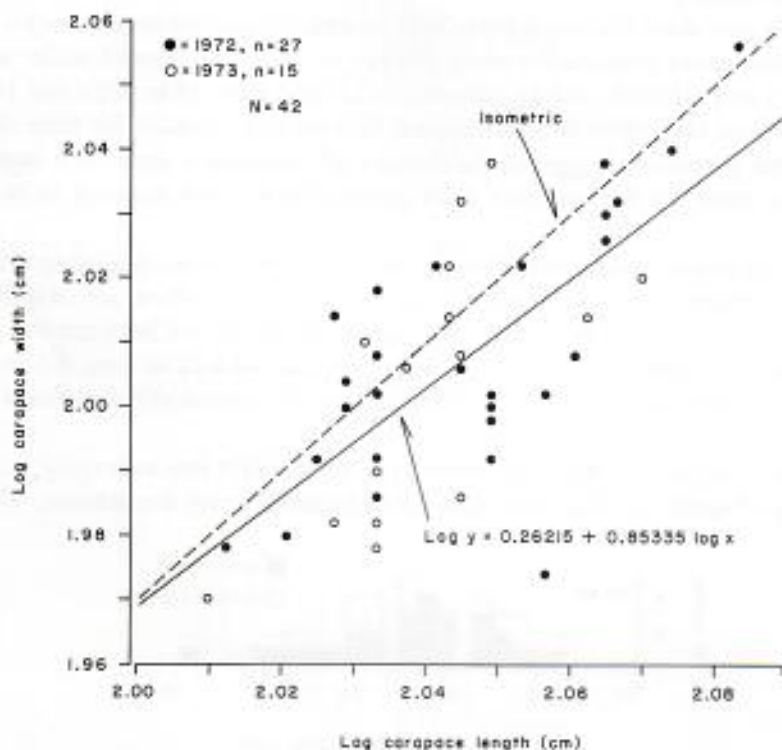Length of the plastron is strongly related to the length of the carapace (for

Figure 13   Relationship between log curved carapace width and log curved carapace length in female *Chelonia mydas* at Mayotte, Comores; showing least squares fitted line and theoretical isometric line.
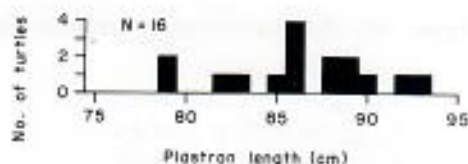
40

Figure 14   Size-frequency distribution for plastron length of female *Chelonia mydas* at Mayotte, Comores; all from 1972 (see also Tables 10, 11 & 12).

log log transformed data: r = 0.67010, d.f. = 14, p < 0.01) (Figure 15). This relationship is not significantly different from isometry (t = −0.91, d.f. = 14, p > 0.1).

Although Mohéli females on average had longer and wider carapaces and longer plastrons than did the Mayotte females, there are no significant differences between the measurements of the two groups (Table 16). The inter-relationships between these body measurements for turtles from the two islands are also similar. For the plot of carapace width on carapace length, using log log
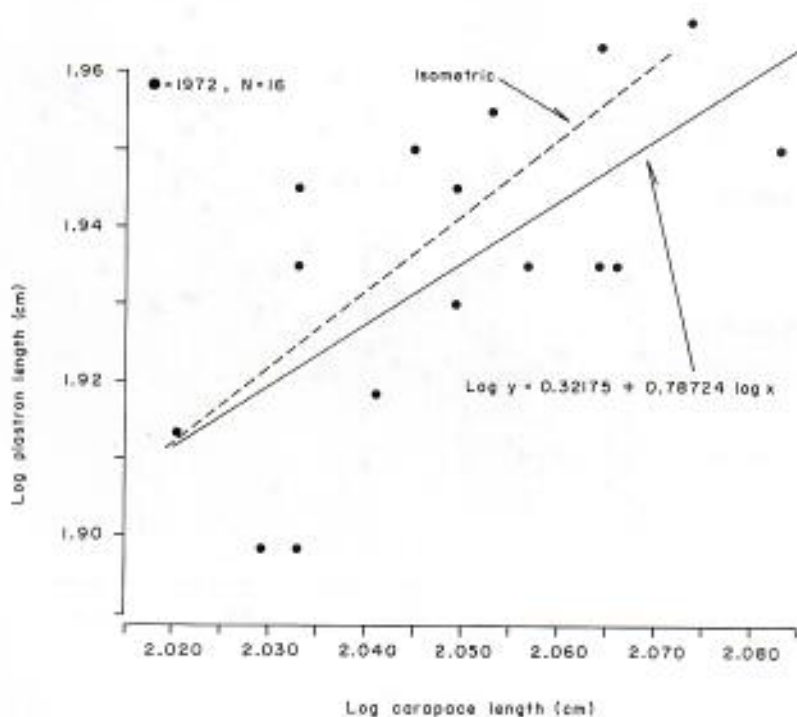

Figure 15   Relationship between log plastron length and log curved carapace length in female *Chelonia mydas* at Mayotte, Comores; showing least squares fitted line and theoretical isometric line.

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transformed data (Figure 16), the analysis of covariance shows no significant difference:

variance ratio $\quad F_{40,50} = 1.03, p > 0.05;$
slopes $\qquad\quad F_{1,90} = 2.78, p > 0.05;$
elevations $\qquad F_{1,91} = 0.57, p > 0.05.$

Likewise, the plot of plastron length on carapace length, for log transformed data (Figure 17), shows that values from the two islands are totally intermingled. The analysis of covariance yields no significant differences:

variance ratio $\quad F_{14,22} = 1.74, p > 0.05;$
slopes $\qquad\quad F_{1,36} = 0.19, p > 0.05;$
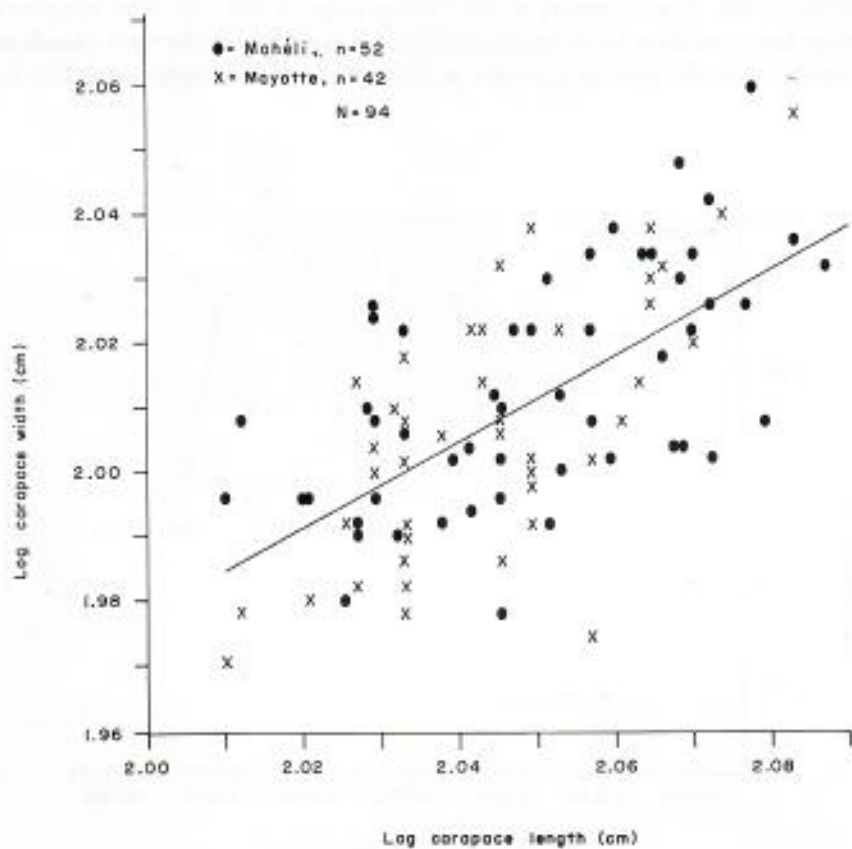elevations $\qquad F_{1,37} = 3.70, p > 0.05.$

Figure 16 Relationship between log curved carapace width and log curved carapace length in female *Chelonia mydas* at Mohéli and Mayotte islands, Comores; showing least squares fitted line.
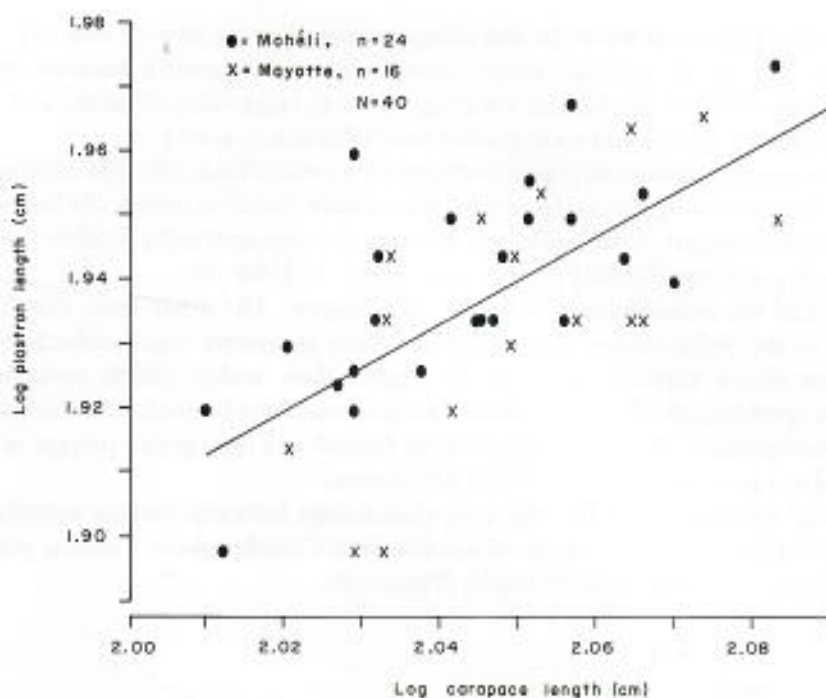
42

Figure 17   Relationship between log plastron length and log curved carapace length in female *Chelonia mydas* at Mohéli and Mayotte islands, Comores; showing least squares fitted line.

On morphometric grounds, the Mohéli and Mayotte females appear indistinguishable.

Hatchlings. Turtles were caught while emerging from nests, and samples from five clutches, distributed over three beaches on Mohéli, were measured (Table 17). Only hatchlings from Clutch 2 were weighed. The average weight was 21.65 g, however, they were not weighed until two days after emerging. On Aldabra, hatchling *Chelonia* lost approximately 1 g per day immediately after emerging (Frazier, 1971: 383), so the values for Clutch 2 may be about 2 g lighter than when the animals first emerged.

Carapace lengths of 36 hatchlings from four clutches on Mohéli averaged 49.18 mm (Table 17). A oneway analysis of variance shows that between clutch variation is much greater than within clutch variation. The animals of Clutch 3 were largest and significantly longer than those from either Clutches 2, 4, or 5 (Table 18).

Carapace widths of these same animals averaged 39.21 mm (Table 17). Again, between clutch variation was significantly greater than within clutch variation, and Clutch 3 was largest, being significantly larger than Clutches 2 or 4 (Table 18).

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Plastron lengths of these 36 hatchlings averaged 40.74 mm (Table 17). A oneway analysis of variance shows considerable heterogeneity between the four clutches (Table 18). Clutch 2 was significantly larger than Clutches 4 or 5, while Clutch 3 was significantly greater than Clutches 2, 4, or 5.

Head width of these hatchlings averaged 15.46 mm (Table 17). The between clutch variation is significantly greater than within clutch variation. As before, Clutch 3 was largest, with significant differences between it and Clutches 2 and 4; Clutch 5 was significantly greater than Clutch 2 (Table 18).

In all of the measurements, Clutch 3 was largest. The other three clutches varied in the order of size, depending on which parameter was involved, but between clutch variation was always greater than within clutch variation. Strictly speaking, the data from these clutches should not be pooled, but despite this heterogeneity, the samples are all from Mohéli and their grand average will be used as a general estimation of this population.

It is of interest to examine the interrelationships between various morphometric parameters. The weights of hatchlings in Clutch 2 show a strong positive relationship with carapace length (Figure 18).
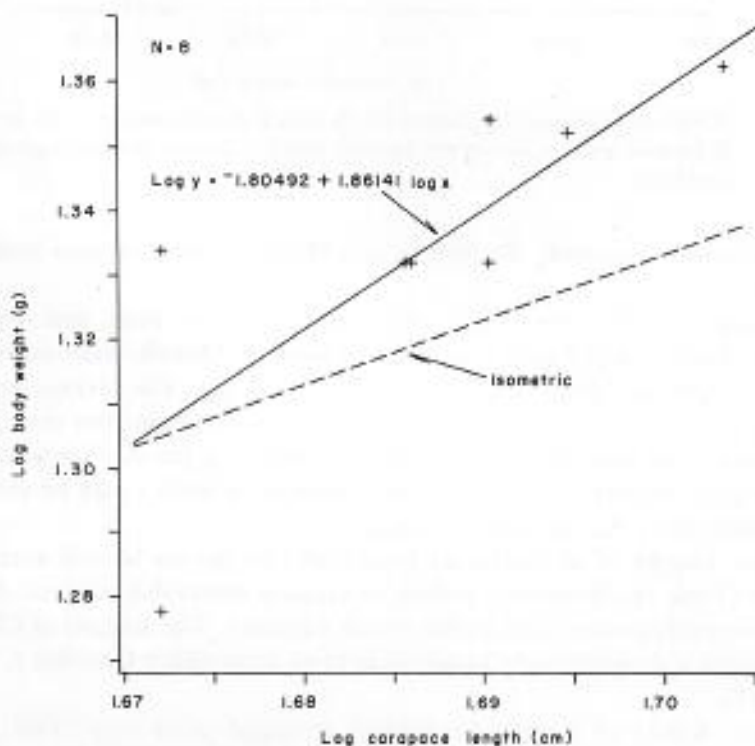

Figure 18   Relationship between log body weight and log straight carapace length in eight hatchling *Chelonia mydas* from Clutch 2 at Mohéli, Comores; showing least squares fitted line and theoretical isometric line (see Table 17).

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The line fitted to these log transformed data has a slope of 1.86141. This is not statistically different from a slope of 1 (t = 1.38, d.f. = 6, p > 0.1), indicating that the weight-length relationship is approximately isometric in newly emerged turtles. However, the conclusion is dependent on this small sample size; the weight-length relationship is generally a power function (Huxley, 1972).

Carapace width shows a positive relationship to carapace length in the hatchlings from Mohéli (Figure 19). This is statistically significant in Clutch 2 (r = 0.82339, d.f. = 6, p < 0.02), but not in the others. An analysis of covariance showed no significant heterogeneity between regression lines for the different clutches:

	linear equations	*log log transformation*
slopes	$F_{3,28}$ = 2.79, N.S.	= 2.91, N.S.;
elevations	$F_{3,31}$ = 2.78, N.S.	= 2.69, N.S.

A significant relationship between carapace width and carapace length is shown by the pooled, log log transformed data (r = 0.54355, d.f. = 35, p < 0.001).
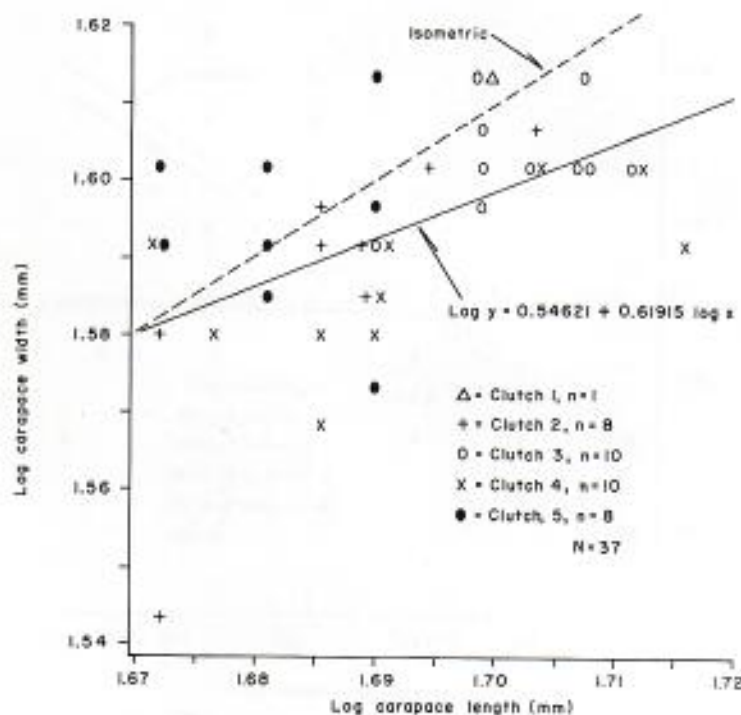

Figure 19   Relationship between log straight carapace width and log straight carapace length in hatchling *Chelonia mydas* from five clutches at Mohéli, Comores; showing least squares fitted line and theoretical isometric line (see Table 17).

The slope of this line (0.61915) is significantly less than 1, the isometric line (t = −2.36, d.f. = 35, p < 0.02), indicating that the width–length relationship in hatchlings is allometric.

Plastron length is strongly related to carapace length in all clutches but number 3; it is statistically significant in Clutches 2 and 4 (r = 0.83851, d.f. = 6, p < 0.01; and r = 0.72799, d.f. = 8, p < 0.02, respectively) (Figure 20). An analysis of covariance indicates that there is no difference in the slopes of lines for the individual clutches, but that the elevations of these lines are different:

	linear equations	log log transformation
slopes	$F_{3,28}$ = 0.25, N.S.	= 0.24, N.S.;
elevations	$F_{3,31}$ = 17.33, p < 0.001	= 17.51, p < 0.001.

The regression line for the pooled data, after log log transformation, has a slope of 0.94738. There is no significant difference between this and a slope of 1 (t = −0.31, d.f. = 35, p > 0.1), indicating that the relationship is approximately isometric.
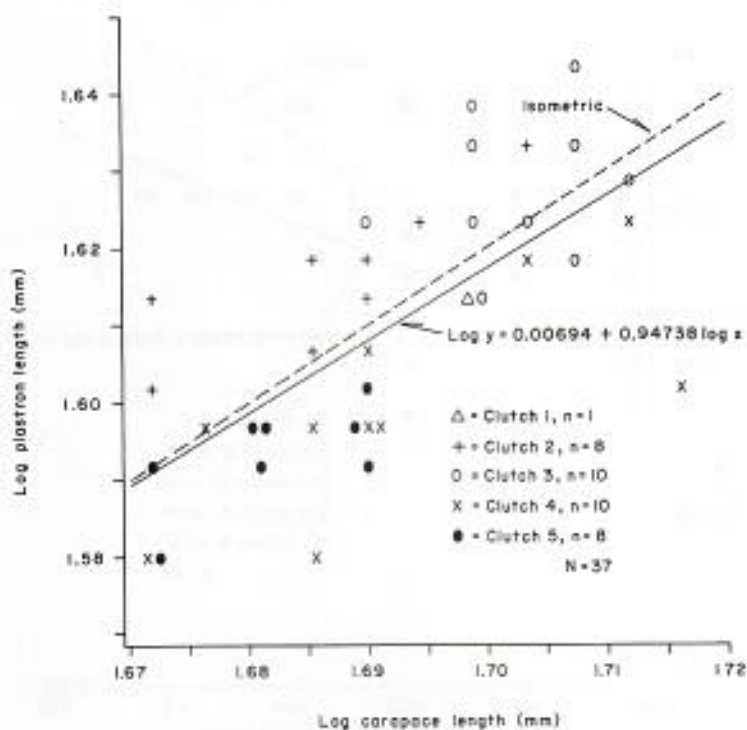

Figure 20   Relationship between log plastron length and log straight carapace length in hatchling *Chelonia mydas* from five clutches at Mohéli, Comores, showing least squares fitted line and theoretical isometric line (see Table 17).

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Head width shows a weak relationship with carapace length (Figure 21). It is significant in only Clutches 2 and 4 ($r = 0.78022$, d.f. $= 6$, p < 0.05; and $r = 0.63753$, d.f. $= 8$, p < 0.05, respectively). An analysis of covariance shows no differences in slopes between the clutches, but a significant difference in elevation is indicated:

	linear equations	log log transformation
slopes	$F_{3,28} = 2.37$, N.S.	$= 2.40$, N.S.;
elevations	$F_{3,31} = 5.41$, p < 0.01	$= 5.47$, p < 0.01.

Although only two of the four clutches have statistically significant regressions, the two parameters are strongly related in the pooled data (for the log log transformed data: $r = 0.50196$, d.f. $= 35$, p < 0.01). The slope of the total data set, 0.48623, is considerably less than 1 ($t = -3.63$, d.f. $= 35$, p < 0.001), indicating that there is an allometric reduction in head width.

The weight data indicate a nearly isometric relationship with carapace length. A similar trend comes from the pooled data on plastron lengths. It is notable, however, that in the largest clutch, number 3, there is no significant re-
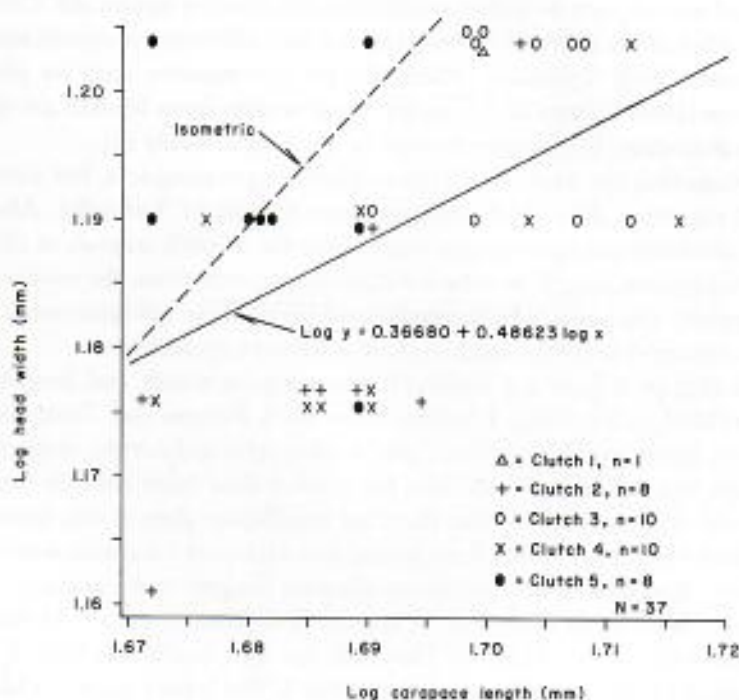

Figure 21   Relationship between log head width and log straight carapace length in hatchling *Chelonia mydas* from five clutches at Mohéli, Comores, showing least squares fitted line and theoretical isometric line (see also Table 17).

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lationship between plastron length and carapace length. If the linear relationship breaks down at large body sizes, it suggests that there may be an allometric change in relative plastron length, although the slope of the pooled data is approximately 1. In the plots of both carapace width and head width with carapace length, the trends have slopes significantly less than the isometric line, indicating allometric reduction. The larger hatchlings have narrower carapaces and heads.

There is a general lack of data for comparing the Mohéli hatchlings with hatchlings from other western Indian Ocean islands. Nearby Aldabra Atoll was reported on by Frazier (1971) and Hughes (1974a) gave information from Europa and Tromelin islands (Table 19). Aldabra's hatchlings were largest of all, with significant differences between the Mohéli hatchlings in all parameters but plastron length. Weights from Europa and Tromelin are greater than those recorded from Clutch 2 on Mohéli. However, considering that the Mohéli weights may be about 2 g light because of the delay in measuring the animals, there may be no significant difference between the weights of these populations (Table 19).

Carapace lengths from Mohéli are larger than those from either Tromelin or Europa, and in comparison with the latter the difference is significant. Carapace widths on Mohéli are narrower, however, but this difference is significant only in comparison with Tromelin. There are no comparative data on plastron lengths from either Europa or Tromelin. Head widths from Mohéli are significantly less than those from either Europa or Tromelin (Table 19).

It is curious that the Mohéli hatchlings have longer carapaces, but narrower heads and carapaces than the hatchlings from Europa or Tromelin. Also, the Aldabra hatchlings are significantly larger than the Mohéli animals in all parameters but plastron length, in which the measurements from the two populations are nearly the same. The interrelationships of these morphometric parameters do not seem to be the same in these different populations.

Hughes (1974a: Figure 12) reported that carapace width and length were strongly related in hatchling *Chelonia* from both Europa and Tromelin, the slopes of the least squares regression lines were 0.5066 and 0.7785, respectively. The Europa line is similar to the line for pooled data from Mohéli (untransformed data: slope = 0.4852), but there are insufficient data to test these lines. Why Mohéli hatchlings would have longer but narrower carapaces is not clear.

Evidently the relationship between plastron length and carapace length breaks down with large body size, as seen in both Clutch 3 from Mohéli and in the pooled data from Aldabra. This indicates that hatchlings have a maximum plastron length, despite overall body size. If this is the case, it could be related to the fact that turtles are 'folded' across the plastron during embryonic development in the typical foetal position. As Ewert (1979: 380) has described, at full term turtles have 'highly contorted fetuses that nearly fill the interior.'

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A newly hatched turtle must 'unfold,' or straighten out before it can locomote and continue to develop normally. Before hatching the embryo must transport the yolk sac into the abdominal cavity. Possibly there is a maximum plastron length above which unfolding or normal embryonic development is impeded, given the restraints of the volume within the egg and the physical problems involved with a growing embryo. Goode & Russell (1968) suggested that in chelid turtles the speed with which the yolk sac is absorbed is related to the position of the embryo within the limited volume inside the egg. Embryos with open access to the plastron could absorb the yolk faster than those that were more tightly packed into the egg.

The embryo's ability to move within the egg could also be important. In a study of the motility of snapping turtle embryos, *Chelydra serpentina* (L.), Decker (1967) reported that both carapace and plastron '...imposed serious restrictions on the activity of the trunk region.' A plastron could be so large that it would inhibit or prevent motility, but it is not known how this might affect the embryo, for certain complex neonatal behaviours seem to occur successfully without the benefit of foetal 'practice' (Smith & Daniel, 1946).

Head width varies little despite differences in body size, although there is a weak relationship in Mohéli hatchlings. Hughes (1974a: Figure 13) presented a plot of head widths on carapace lengths for 50 hatchling *Chelonia* from Europa; this showed considerable variation, but no analysis was presented. These observations indicate that there is a minimum head width. In vertebrates the head grows to full embryonic size before the trunk, and variation in head size is less than in sizes of other, postcephalic body parts. A hatchling turtle may not function efficiently without a critical mass of nervous tissue, particularly that related to olfactory and optic facilities, while variations in amounts of postcranial tissues may be less critical. Discussions of the embryonic and adaptive implications of the cephalo–caudal law of embryogenesis are many (see review in Ewert, 1979 and Huxley, 1972: 132 ff., for a discussion of the 'Law of Antero-posterior Development').

Growth and Size Comparisons

Eight hatchlings from Clutch 2 on Mohéli were taken to Moroni, Grande Comore and reared by Phillipe Richeux. The holding tank was about 1 m² and held about 20 cm of seawater; it was out-of-doors and shaded, and the turtles were fed chopped fish daily. Animals 1, 2, and 6 were given away early in the experiment. Number 8 died after approximately one month; number 4 died after approximately two months. Both of these animals were preserved by drying. Animals 3, 5, and 7 were measured alive on 30 June 1972, when they were three months old. As the ages of numbers 4 and 8 are uncertain, and as small changes in body proportions (especially head widths) may have occurred on

drying, the final measurements for these two animals should be taken as approximate (Figure 22).

The changes in body measurements that occurred after three months indicate: 1) carapace length increased about 0.4 mm per day; 2) carapace width increased about 0.3 mm per day; 3) plastron length changed slightly more slowly; and 4) head width increased less than 0.1 mm per day. The weights of three animals (numbers 3, 5, and 7) increased from 21.5, 22.6 and 22.5 g respectively, to *over* 100 g each (exact weights were not obtained because the maximum of the balance was 100 g). This is an increase of at least 80 g in three months, or *at least* one gramme per day. These rates of increase are comparable to those of other studies of growth under captive conditions (cf. Frazier, 1971: Fig. 4; Lebeau & Lebrun, 1973).

As these animals grew longer, they grew relatively wider. The slope of the regression of log carapace width on log carapace length is 1.0876, and this is significantly greater than the isometric slope of 1 ($t = 4.71$, d.f. $= 8$, p $= <$ 0.002) (Figure 23).

These five hatchlings showed relative shortening of the plastrons as their car-
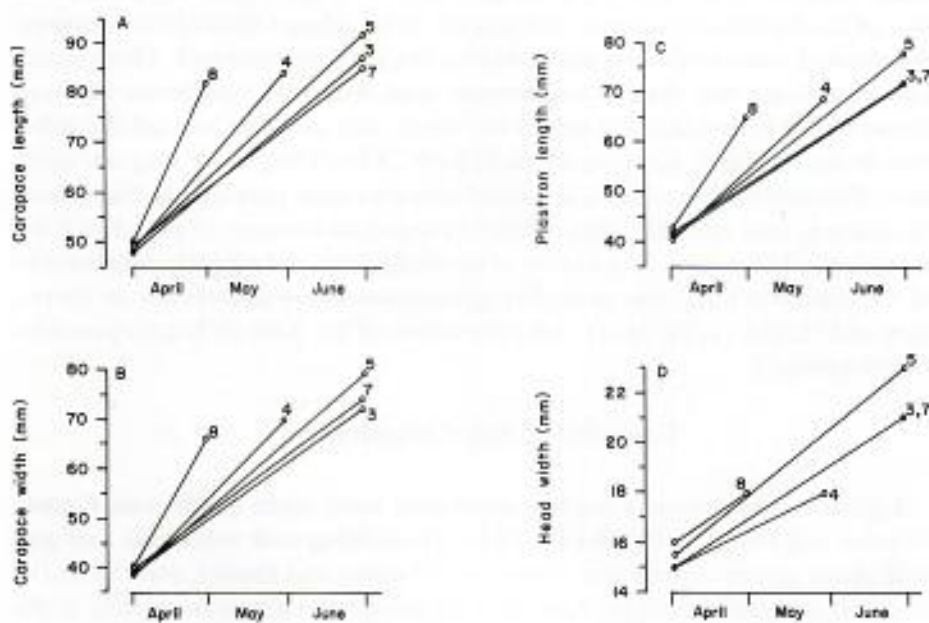

Figure 22   Increase in body measurements of five captive-reared *Chelonia mydas* from Clutch 2, Mohéli, Comores: A – Straight carapace length; B – Straight carapace width; C – Plastron length; D – Head width; all measurements in mm; (individual turtles are indicated by the numbers: 3, 4, 5, 7 and 8), ages of animals numbers 4 & 8 are not certain.
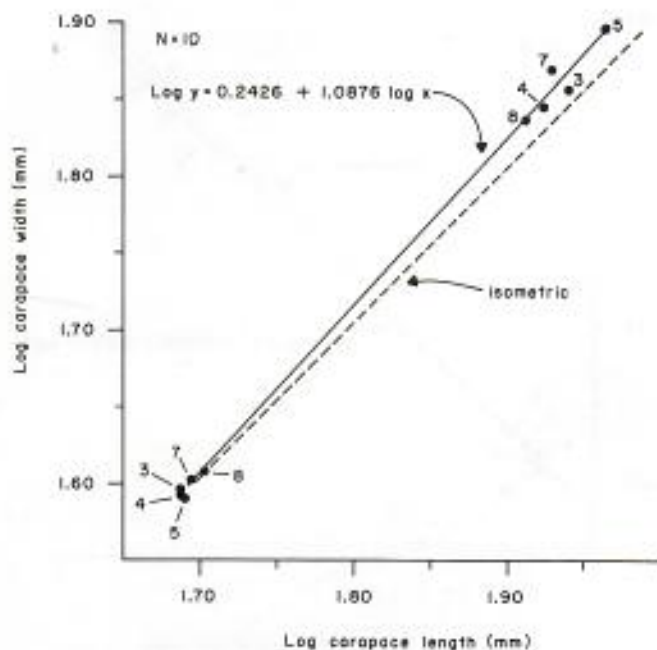
Figure 23   Change in log straight carapace width with increasing log straight carapace length in five captive *Chelonia mydas* from Clutch 2, Mohéli, Comores, showing least squares fitted line and theoretical isometric line; (individual turtles are indicated by the numbers: 3, 4, 5, 7 and 8).

apaces grew longer. However, this trend was not significantly different from isometry ($t = -1.37$, d.f. $= 8$, $p > 0.1$) (Figure 24).

Relative head width also decreased with increasing carapace length. This reduction was very different from the isometric condition ($t = -12.75$, d.f. $= 6$, $p < 0.001$) (Figure 25).

Comparisons between individuals are sometimes used to investigate changes that occur during growth, but these comparisons must be interpreted with care. The growth data on hatchlings show that an individual's carapace becomes relatively wider as it increases in length, but in hatchlings and adult females the longer carapaces are relatively narrower (Table 20). Hence, the ontogenetic change within individuals is not always reflected by comparisons between individuals.

Plotting all of the Mohéli data on log carapace width vs log carapace length shows an overall increase in relative carapace width, from hatchlings to adults; the predictive line is significantly steeper than 1 ($t = 15.01$, d.f. $= 97$, $p < 0.001$) (Figure 26). A simple linear equation accounts for a major portion of the scatter ($R^2 = 0.99944$, $F_{1,97} = 171,616.97$), however the relationship may be more complicated. The predictive line fits most of the data points very well,
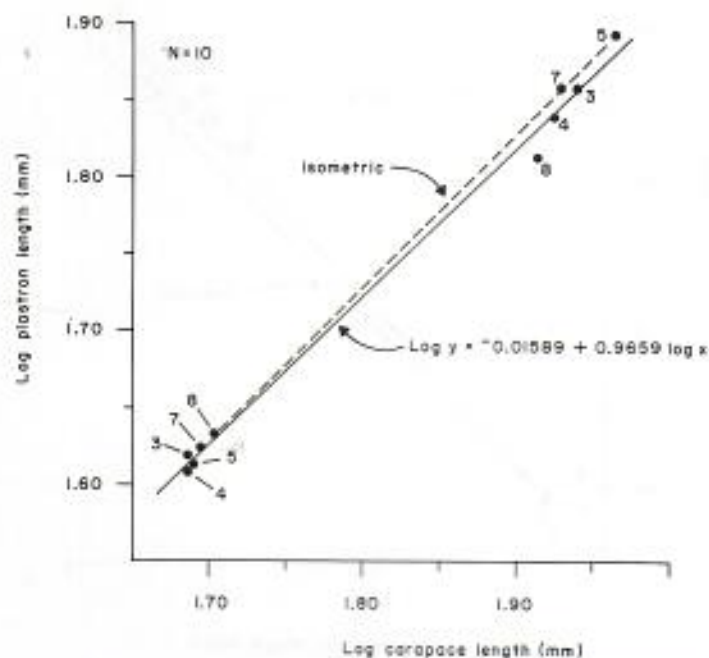
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Figure 24   Change in log plastron length with increasing log straight carapace length in five captive *Chelonia mydas* from Clutch 2, Mohéli, Comores, showing least squares fitted line and theoretical isometric line (individual turtles are indicated by the numbers: 3, 4, 5, 7 and 8).

but the immatures, at about the middle of the line, are noticeably above it. The curve appears steep from hatchlings to immatures, then decelerates below 1. This indicates allometric acceleration followed by allometric reduction and conforms to the general field impression of changes in turtle shapes as the animals get larger; however, more data from immatures, at the middle of the line, are necessary to confirm this.

Changes in relative plastron length with the different data sets are consistent from one group of measurements to another. Individual growth in hatchlings shows an allometric reduction, and plots between hatchlings and between adult females show that larger animals have relatively shorter plastrons (Table 20). All of these data taken together indicate a curve which is below the isometric line ($t = -6.77$, d.f. $= 66$, $p < 0.001$) (Figure 27). The reduction is most marked in animals larger than immatures, and especially notable in the single male plotted (below the cluster of points for nesting females).

Relative head width also shows a consistent trend: growing hatchlings, comparisons between individual hatchlings, and comparisons between animals of various sizes all show conspicuous decreases in relative head width (Figure 28). The curve is well below the isometric line ($t = -39.00$, d.f. $= 40$, $p < 0.001$).
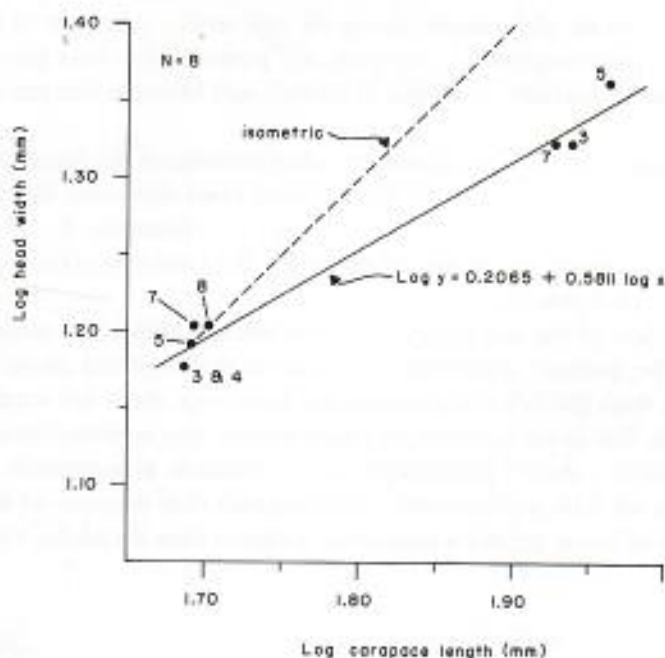
Figure 25   Change in log head width with increasing log straight carapace length in three captive *Chelonia mydas* from Clutch 2, Mohéli, Comores, showing least squares fitted line and theoretical isometric line (individual turtles are indicated by the numbers 3, 4, 5, 7 and 8).

For Mayotte the few comparisons that can be made are between nesting females. These indicate an allometric increase in both carapace width and plastron length with increasing carapace length; however, a larger range of values is likely to show changes consistent with those that occur at Mohéli.

All of these changes in relative body proportions have been described in *Chelonia* at nearby Aldabra Atoll: narrowing of the carapace, shortening of the plastron and narrowing of the head (Frazier, 1971: 383 ff.). These types of allometric changes probably occur throughout the range of the species.

Scalation

Each of the three immatures examined (Table 6) had normal scalation of the carapace, plastron, postoculars, axillaries and inguinals. Number 787, however, had 6 vertebrals, which is not usual. No data on scalation were recorded for either of the two males. The scalation of females from Mohéli and Mayotte is summarized in Table 21. The most common ('normal') condition is: cervical – single; vertebrals – five; supracaudals – one pair; pleurals – four pairs; marginals – eleven pairs; inframarginals – four pairs; intergular – single and large; gulars,

humerals, pectorals, abdominals, femorals, and anals – one pair of each; axillaries – three pairs; inguinals – one pair; and postoculars – four pairs. The size of the postanal is variable. Scalation of Mohéli and Mayotte females is comparable.

In the main, these scale conditions are characteristic of the species, but rarely have they been reported in detail. Information from five other localities in the western Indian Ocean Region (viz., Europa Is., Tromelin Is., St. Brandon Islands, Mozambique and South Africa) show the same characteristics of scales (Hughes, 1974a: Table 2).

The scalation of the hatchlings from five Mohéli clutches is summarized in Table 22. The 'normal' condition is the same as that reported above with nesting females, with the following exceptions: hatchlings show less variation in inframarginals, but more variation in inguinals and also in postoculars. The animals of Clutch 3 show considerably more variation in marginals, but more constancy in pleurals, axillaries and inframarginals than do some of the others.

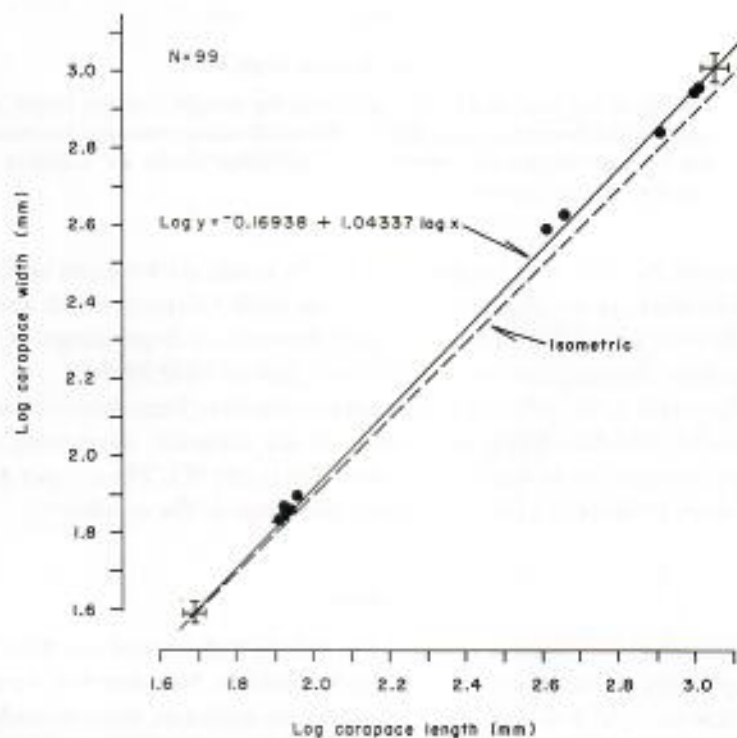If hatchlings show greater variation in scalation than do adults, this indicates

Figure 26   Change in log carapace width with increasing log carapace length in *Chelonia mydas* at Comores, showing least squares fitted line and theoretical isometric line; average (± t standard deviations) for hatchlings and nesting females are shown by crosses at bottom and top of line.
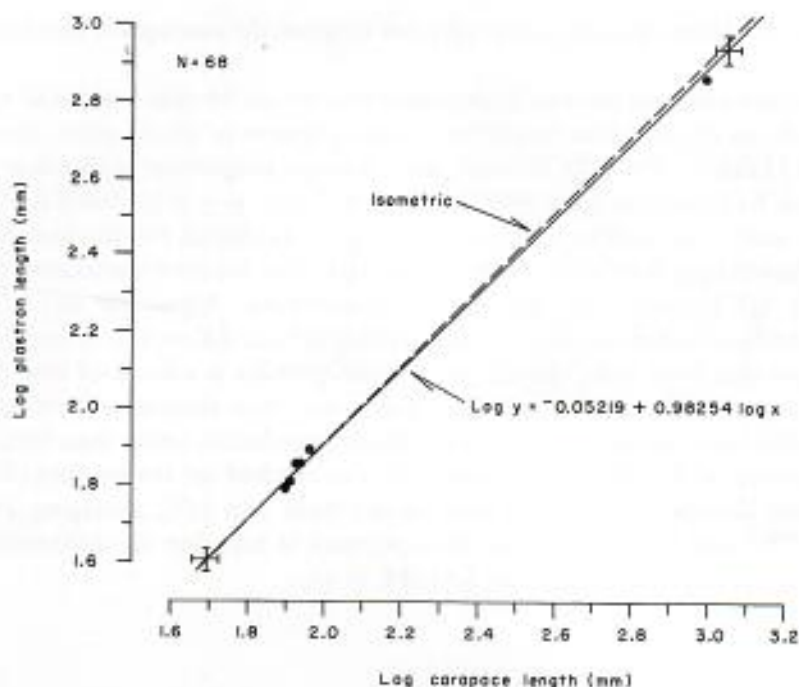
Figure 27   Change in log plastron length with increasing log carapace length in *Chelonia my-das* at Comores; showing least squares fitted line and theoretical isometric line; averages ($\pm$ t standard deviations) for hatchlings and nesting females are shown by crosses at bottom and top of line.

that stabilizing selection may be in operation. Individuals with characteristics away from the norm may be at a selective disadvantage. However, to corroborate this process, as opposed to ontogenetic normalization, it is necessary to show that the scale characteristics of an individual do not change as it grows and matures, as Gadow (1899) once claimed.

Coloration

The three immature *Chelonia* examined (Table 6) had carapaces marked with conspicuous chestnut-red blotches and a dominant pattern of raying. The scales on the dorsal surfaces of the limbs, head and neck were likewise dominated with the chestnut (Plate VIII). This pattern is absolutely typical of immature *Chelonia* in the western Indian Ocean.

The adult males seen while skin diving at Mayotte were coloured with black spots and did not have conspicuous amounts of chestnut-red pigment or pigment distributed in rays. The carcass from Ouallah, Mohéli (JFCm 797), presumed to be male, had a black spotted carapace. This pattern is characteristic of

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males on Aldabra (Frazier, 1971: 390) and supports the assumption that 797 was a male.

The coloration of females from several beaches on Mohéli was noted. Of 40 animals, 92.5% had concentrations of dark pigment in all, or some, carapace scutes (Table 23; Plates IX through XII). A larger proportion of live than dead animals had concentrations [$\chi^2(G) = 6.54$, d.f. $= 2$, $p < 0.05$, Sokal & Rohlf, 1969: 599]. Thirty-eight of these females were examined for the presence of chestnut-red pigment in the centre of the dark concentration mentioned above (Table 24). In total, 76% showed this characteristic. Again, the live animals showed the coloration more strongly [$\chi^2(G) = 7.02$, d.f. $= 2$, $p < 0.05$]. This suggests that scute color changes after death, perhaps as a result of desiccation or exposure to the sun. If this assumption is true, then chestnut-red centres are probably found in 95% of the nesting female population, rather than 76%.

Thirteen of the above specimens were also checked for the amount of dark pigment distributed in rays. Values ranged from 5 to 95%, averaging 47.3% ($\pm$ 7.8%), and live animals had more pigment in rays, but the difference was not significant ($F_{4,7} = 1.49$, $t = 1.85$, d.f. $= 11$).
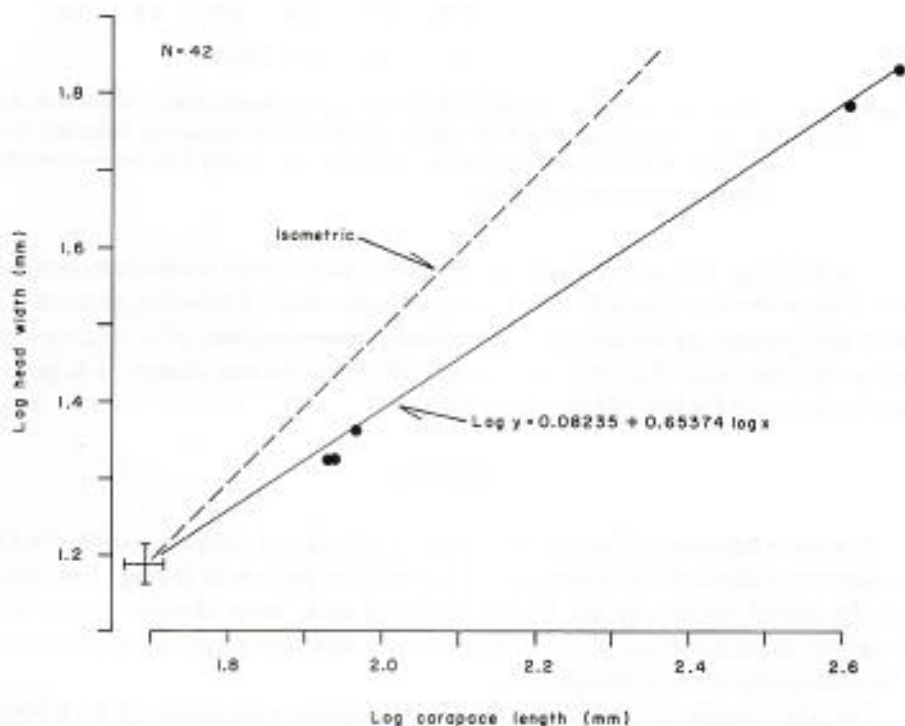

Figure 28   Change in log head width with increasing log carapace length in *Chelonia mydas* at Comores; showing least squares fitted line and theoretical isometric line; average ($\pm$ t standard deviations) for hatchlings is shown by cross at bottom of line.

Females examined at Mayotte were also colored similarly to females at Mohéli. All of the 38 specimens examined had at least some pleurals with concentrations of dark pigment, and 84% had concentrations in all scutes (Table 23). If coloration is changing after death, as seems to happen on Mohéli, this value will be low, but sample sizes are too small for comparing live vs dead for 1972. There was no significant difference between the observations of 1972 and 1973 [$\chi^2(G) = 1.72$, d.f. = 2, p > 0.05].

Of the 29 specimens examined, 93% showed the presence of chestnut-red pigment within concentrations of all or some scales; 86% had this coloration in all scales (Table 24; Plate XIII). However, this figure may be low if there is colour change after death. There is no significant difference between 1972 and 1973 [$\chi^2(G) = 2.78$, d.f. = 2, p > 0.05]. Two animals had 75% and 60% of the dark pigment outside the concentrations distributed in rays.

There is no evidence for any population differences between the coloration of the Mohéli and Mayotte turtles. Comparing Mohéli females with those from Mayotte in respect to scores for scutes with concentrations of dark pigment gives a $\chi^2(G)$ of only 2.26 (d.f. = 2, p > 0.05). Scores for scutes with chestnut-red centres also show no significant difference [$\chi^2(G) = 3.90$, d.f. = 2, p > 0.05].

In summary, almost all females had at least some carapace scutes with conspicuous dark concentrations of pigment; the majority – possibly the vast majority – also had chestnut-red centres to these concentrations, and a considerable amount of pigment outside the concentration was arranged in rays and not spots. These observations are similar to those made on nesting females at Aldabra Atoll (Frazier, 1971: 390).

The same hatchlings as those measured (see Section on Morphometrics) were also observed for characteristics of coloration. As usual for the species, they were dark above and light below. The only quantified observation relevant to hatchling coloration was the position of the beginning of the *solid* white border on the marginal scales (Table 22). The most common position is the posterior of the third marginal, but it can begin as far forward as the middle of the second and as far back as the anterior of the fourth.

Body Condition

One of 16 Mohéli females had major damage to a front flipper; one of 19, had major damage to a hind limb. No animals with damaged shells were seen, except JFCm 730 which had broken supracaudals (Tables 7 & 8).

One female at Mayotte had the left hind limb stumped and the posterior of the plastron (anal scales) highly asymmetric. The proximity of the two abnormalities indicated that they might be related, possibly from an accident when

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the animal was small (Plate XIV: Figure 1). A second female had a 'hunch-backed' carapace.

Feeding Habits

Samples of stomach contents from four nesting Mohéli females (JFCm 795, 854, 857 and 858) and one animal presumed to be a male (JFCm 797) were examined. In all instances the contents were marine plants, algae and angio-sperms. More detailed analysis on samples from JFCm 854, 857 and 858 are shown in Table 25. At Mayotte *Chelonia* were seen over or near marine pas-tures both in the lagoon and on the seaward fringe. Stomach contents from four nesting females slaughtered on Pamanzi Island showed *Thalassodendron ci-liatum*, several species of brown algae, small gastropods, and small pebbles. In general, stomachs and intestines that were examined contained very little. Un-fortunately, the samples were lost, but the predominance of plant material is normal for adults of this species. The absence of conspicuous animal matter and a preponderance of *Thalassodendron ciliatum* is the norm for adult *Chelonia* in the western Indian Ocean, and the feeding habits of the Comoro *Chelonia* are comparable with what is known from other parts of the species' range (cf. Fer-reira, 1968; Frazier 1971: 394; Mortimer 1976).

Breeding Biology

Mating behaviour. Information on mating behaviour at Mohéli is limited to sightings of copulations which were recorded from 26 February to 1 April 1972 (Table 5). As pointed out earlier, there were no observations in June 1972 when nesting was most intense. A male at Bangoi-Kouni, Grande Comore, on 24 May 1973, approached us while underwater, indicating that depending on the availability of receptive females, mating could occur as late as the end of May. No copulations were seen at Mayotte, but single males often approached me while I was swimming off of Moya beach in late May and early June 1972. They were curious and almost aggressive, apparently searching for mates. Five males were seen milling around a single female, evidently trying to mount her. Mating is evidently seasonal, occurring before the peak in nesting. This is con-sistent with findings elsewhere (Frazier, 1971: 377; Booth & Peters, 1972: 809).

Thirty-four Mohéli females were scored for the condition of their copula-tion marks (notches cut into the females' third marginals by the pollex claws of the mounted males). As the nesting season progressed, there was an increase in both the occurrence and size of these marks (Figure 29).

Copulation notches were scored for 14 Mayotte females, 13 of which were at Pamanzi in June 1972. The preponderance of animals had conspicuous
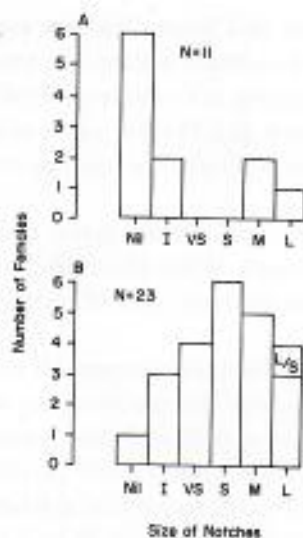
Figure 29   Seasonal changes in copulation notches of *Chelonia mydas* at Mohéli, Comores: A
– February and March, B – June. Sizes of notches are indicated as follows: Nil =
no notches or irritations, I = irritations but no notches, VS = very small, S =
small, M = medium, L = large, L/S = large notch on one side/small notch on
the other.

marks: 1 – large; 9 – medium; 1 – small; 1 – very small; 1 – irritations only; 1
– no marks. This is comparable to the situation on Mohéli in June.

   If it is assumed that mating *always* results in copulation marks, then it would
seem that females nesting early in the season are laying *before* they have copulat-
ed. However, given the information on the timing of mating season presented
above, this seems unlikely, and it would appear better *not* to assume that mating
always results in copulation marks (see Frazier, 1971: 377). Rather, copulation
notches, which are cut into bone about two cm thick, are more likely the result
of multiple copulations, numerous occasions of weakening the bone through
several mountings. The creation of these notches could be further facilitated by
a calcium deficit: laying large clutches (hence using a large amount of calcium
in egg shells) and not feeding during the nesting season could easily produce
this deficiency.

   Booth & Peters (1972: 809) and Wood & Wood (1980: 500) indicate that a
female mates only once in a season, but the observations reported do not dis-
prove multiple matings. In other studies, it is reported that males court and
mount females as they enter the sea after nesting. Also, the fact that copulation
marks can be asymmetrical suggests that whenever a notch is cut it is not sim-
ply a matter of being mounted; an animal bearing a notch on the left but none
on the right would be scored from the left as post-copulatory and from the

right as precopulatory! The data from Comores suggest a peak in mating before the peak in nesting and multiple matings for females.

The diurnal pattern of mating at Comores is similar to that described in other studies (Hendrickson, 1958: 482; Frazier, 1971: 375 ff.); the majority of copulations occur before midday. Of nineteen separate copulations, 14 occurred before noon (Table 5).

Copulations were observed off all the major rookeries but notably around the offshore islands in the south. While this is likely to be the result of observer bias, it is also probable that the large area of protected shallow water is an attractive mating ground.

With the exception of three observations, all records of copulations were within 500 m of shore, whether this involved the main island or the offshore islands (Table 5). Other studies indicated that copulations occur within a few hundred metres of shore (Hendrickson, 1958: 481; Frazier, 1971: 375), but such information is clearly subject to observer bias as most observers are shore based.

Of the 19 separate copulations observed, at least seven had 'escorts.' The sex of these animals was only confirmed on two occasions, but it is assumed that all escorts were males, because females do not seem to exhibit this behaviour. On three occasions there was only one escort, while on three other occasions there were from four to six (Table 5). As Booth & Peters (1972: 810) have pointed out, as many as five males may congregate around a mated pair – even if females outnumber males. Hence, efforts to estimate sex ratios of breeding populations from numbers of escorts (e.g., F.A.O., 1968: 35; Hirth & Carr, 1970: 40) are misleading (see also Hughes, 1974a: 12).

Males are competing for receptive females, and they will eagerly explore objects they perceive as potential females. They may approach a human swimmer or a small boat, as was experienced at both Grande Comore and Mohéli. Booth & Peters (1972: 809) also relate this exploratory behaviour for males in Australia.

Nesting season. At Mitsamiouli, Grande Comore, there are two records of nesting, both by Mr. Chevalier: a nest emergence in September, 1971 (from a nesting presumably in July) and a nesting in January 1972. The male(s) sighted underwater on 24 May 1973 off Bangoi-Kouni, in the north, was evidently attracted to swimmers and was probably searching for receptive females.

It would be stretching the data to claim that the nesting season at Grande Comore extends from January to July (or from July to January), for nesting is too sporadic to really qualify for a nesting season. More likely, the situation at Grande Comore is best described by saying that nesting can occur at least from January to July, but infrequently at any time. That it occurs during the first half of the year and not the second is inferred from the situation on Mohéli, Mayotte (see below), and Aldabra (Frazier, 1971: 375; Gibson, 1979).

There are considerable data from Mohéli (Tables 7, 8, 9), and it is clear that

nesting lasts from late February until at least late June. In the light of the generalized breeding biology that is typical of the species throughout its range (see Frazier, 1971: 379; Hirth, 1971: 3: 4; 1980), it is possible to deduce a longer nesting season. Nest emergences the nights of 30 and 31 March, at beaches 47 and 45, respectively (Table 9), indicate nestings in late January (i.e., two months before nest emergences). Three females killed on nesting beaches, numbers 8 and 12, on the night of 26 June (Table 8) had enlarged follicles that were probably to have been laid about two weeks late. Female JFCm 858 had two follicle sizes, so presumably she would have laid twice at about two-week intervals, first in early July and second at the end of the month. There is little doubt that the nesting season at Mohéli extends at least from late January to late July.

It is clear from seasonal changes in the amount of nesting spoor on Mohéli beaches, i.e., the numbers of females beaching nightly and the number of nest emergences in a night (Table 9), that there is an increase in nearly all Mohéli beaches from February to March and again from March to June. For the month of April data are only available for the first day, and none are available for May. However, working back from the dates of nest emergences to two months earlier (inferred date of laying), it appears that nesting was nearly as active in April as it was in June.

Evidently the nesting season at Mohéli peaks in about June, having begun at least in January, so it may continue for a large part of the year. This is consistent with anecdotal information I was given by residents, and comparable with the seasonality on Mayotte, Aldabra (Frazier, 1971: 410; Gibson, 1979), and Maziwi Island, Tanzania (Frazier, in prep.) but not with that on Europa, Tromelin and St. Brandon Islands (Hughes, 1974a: 14). On Aldabra nesting occurs year round with a peak in the austral winter. It occurs at least ten, and most probably twelve months on Maziwi, also peaking about the same time. On Europa, Tromelin and St. Brandon, Hughes claims that nesting is year long, but the peak is in the austral summer.

The information regarding a female nesting at Mirontsi, Anjouan in 1969 did not include the month, so nothing can be said of the nesting season on that island. It seems likely that what little nesting does occur would coincide with the peak at Mohéli.

At Mayotte recent nesting was recorded at the Moya beaches from 7 April until 10 June 1972, and on 18 June 1973. From the condition of the spoor, it was clear that nesting occurred from at least late February. A female with two sizes of enlarged follicles, that nested on 8 June, probably would have nested twice again, in the end of June and in mid July. Mayotte's nesting season is evidently similar to that on Mohéli and Aldabra, where there appears to be a peak during the trade winds, from May to August. There may be nesting throughout the year.

Nesting behaviour. Seven Mohéli females were observed during their nest-

ing activities (Table 26) and more than a dozen others were seen in various stages of nesting (Table 27). A few Mayotte females were also observed, but with an emphasis on tagging and censusing, few detailed observations could be made on nesting behaviour. Yet the nesting process in Comores is typical of the species (see Table 26; Plate XIV: Figure 2; and Frazier, 1971: 379).

Many of the times presented in Table 26 are approximate, so the data are applicable only for a preliminary statement. Beaching times seem to be related to the time of high tide (and hence to state of tide – spring or neap). During spring tides, which are full just after dusk, the animals are leaving the sea a few hours after dusk; during neap tides, which are full about midnight, they are beaching just after midnight. During neaps, ten of eleven records are before high tide; all of the three spring tide records are from after the high tide. Beachings during neap tides also occur nearer to the time of high tide than do spring tide beachings. All beachings at spring tides are more than two hours after high tide; all beachings during neap tides are less than two hours (and many are less than one hour) from high tide.

The timing of beachings, near to high tide, is most probably related to access to the beach and ease in getting up the beach face. The fact that neap tide beachings precede the high tide and are closer to it may be because the high neap tide rises very little, and to get its full benefit the animals must be on time.

It is possible that there is also a social stimulus affecting the animals to aggregate off the rookery and nest together. This would swamp predators and also function in spacing nests out, reducing nest destruction by the females themselves.

All beachings occurred at night, which is a rarely broken rule with this species. Female JFCm 713 did leave the sea just before daybreak on beach N° 45 and laid during daylight. Daylight nestings that do occur are known from remote areas where there is seldom disturbance by humans (see Hirth, 1971: 3: 4). The west beach of Chissioua Ouénéfou (beach number 45) is in fact remote and undisturbed by people or predators large enough to bother a female *Chelonia*.

All beachings at Mayotte were also at night, but one animal (JFCm 720) nested, apparently undisturbed, while it was photographed with several powerful lights. The left hind flipper of this same animal was stumped, and useless in sand excavation, yet it used alternate strokes of the hind limbs. Another curious observation was made on female JFCm 717 on the 5th of June. She spent 24 hours upside down on the beach, and on being turned right side up proceeded to nest and lay 31 eggs.

Nesting periodicity. While there is no direct information on this topic at Comores, there is sufficient information to infer that *Chelonia* nests about three times a season on Mohéli and Mayotte (there are no relevant data from either Grand Comore or Anjouan). Mr. E. Laurette of Fomboni, Mohéli, speaking from considerable experience, claimed that females typically have many

hundred yolked eggs. Three Mohéli specimens slaughtered by local peoples on beaches 8 and 12, all on the night of 26 June 1972, confirmed this. Female JFCm 854 contained many large follicles (15 to 20 mm in diameter) in the body cavity; presumably it had laid before it had been killed, for no shelled eggs were found. Female JFCm 857 had 157 shelled eggs and large numbers of small follicles (10 mm or less in diameter). Female JFCm 858 had 158 shelled eggs and large numbers of follicles of two sizes (about 15 to 20 mm and about 10 mm or less). A complement of three clutches is clearly indicated by the latter.

Similar evidence is available from Mayotte. Female JFCm 825 had a full complement of shelled eggs as well as large numbers of enlarged follicles of two sizes; females JFCm 820 and 826 each had shelled eggs and over 100 large follicles. Other well documented studies indicate one female may lay as many as seven clutches per season (cf. Frazier, 1971: 379; Hirth, 1971: 3: 4), although there is some disagreement as to whether the counting technique is valid (Schulz, 1975: 71).

Site tenacity. This species shows an uncanny ability to return to the same beach area for repeated nestings. The behaviour has been well documented in Sarawak, Borneo (Hendrickson, 1958: 497), Tortuguero, Costa Rica (Carr & Carr, 1972), Ascension, South Atlantic (Carr, 1975: 552) and Surinam (Schulz, 1975: 75), and it seems to be the norm for the species. It is assumed that *Chelonia* at Mohéli and Mayotte exhibit site tenacity also, and that each major nesting beach has a group of turtles that returns regularly to nest on it.

Clutch size. In seven Mohéli clutches, the number of eggs varied from 85 to 158, averaging 122.44 ($\pm$ 9.95) (clutch size was determined by counting eggs as they were laid, by allowing each egg to pass through my hand on its way from the turtle's ovipositor to the egg hole, or by counting eggs that were found within the body cavity of a slaughtered female). Five Mayotte clutches varied from 104 to 139 eggs, with an average of 121.6 ($\pm$ 7.325); JFCm 820 with 138 eggs, had 151 enlarged follicles, and JFCm 826 had 108 eggs with over 100 enlarged follicles. These values are similar to the Tromelin average (129) but less than that from Europa (152) (Hughes, 1974a: Table 19a).

The Mohéli clutch size data are distributed in four 'clumps': 85 to 86 (two clutches); 101 to 109 (two); 120 to 128 (two); and 157 to 158 (three). As both large and small clutches were laid on both eastern and western beaches and in both early March and late June, there is no obvious season or locality effect. There does, however, appear to be a positive relationship between carapace length and clutch size, although it is not statistically significant ($r = 0.53959$, d.f. $= 6$) (Figure 30). There is no significant relationship between Mayotte clutch sizes and carapace lengths ($r = 0.42531$, d.f. $= 3$, $p > 0.1$).

Hughes claimed (1974a: 16) that there was no such relationship on Europa, but that female length and clutch volume and/or weight ($=$ mass) were related on Tromelin. However, his Europa data (his Figure 21) could be interpreted in
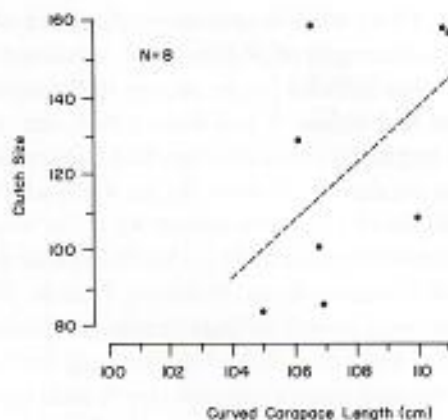
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Figure 30   Relationship between clutch size and curved carapace length in *Chelonia mydas* at
Mohéli, Comores; least squares fitted line (y = 7.32559x − 667.77302) is not signif-
icant.

another way: along with random error there is probably the effect of serial
clutch number on clutch size; clutch size may well diminish from first to last
clutch, and these factors must be reckoned with. The positive relationship be-
tween female length and clutch size seems to occur in means of different popu-
lations (Frazier, 1971: 380), and it is suspected to occur in individuals within a
population (see also Hirth, 1980).

Egg size. Samples of ten eggs (chosen at random) from each of two Mohéli
clutches and each of four Mayotte clutches were measured (Table 28). Mohéli
diameters vary from 41 to 45 mm and calculated egg volumes vary from 38.8
to 46.7 cm³. Calculated clutch volumes were 6,600 and 6,726 cm³.

At Mayotte eggs within a clutch showed little variation, but there was con-
siderable difference between clutches. The eggs from female 720 were about
half the weight of those from the other three females, so they will be discussed
separately. In the remaining three turtles, egg diameters ranged from 42.5 to
48.0 mm. Individual egg weights varied from 48.0 to 60.0 g, and the clutch
averages ranged from 50.2 to 56.8 g. Calculated volumes of individual eggs
varied from 42.6 to 56.7 cm³, and averages for each of the three clutches in-
creased from 44.8 to 53.2 cm³. The calculated clutch volume for female 820
was 6,297 cm³. There is 100% correlation between female size and egg size in
these three animals (Figure 31).

These calculated volumes are comparable with the volumes reported for
Tromelin (evidently actually measured), which were found to vary with the
length of the female (Hughes, 1974a: Table 20). Egg diameters are likewise
comparable with the values reported for Tromelin and Europa (Hughes, 1974a:
Table 19a), but less than the Aldabra figure (Frazier, 1971: Table 2). However,
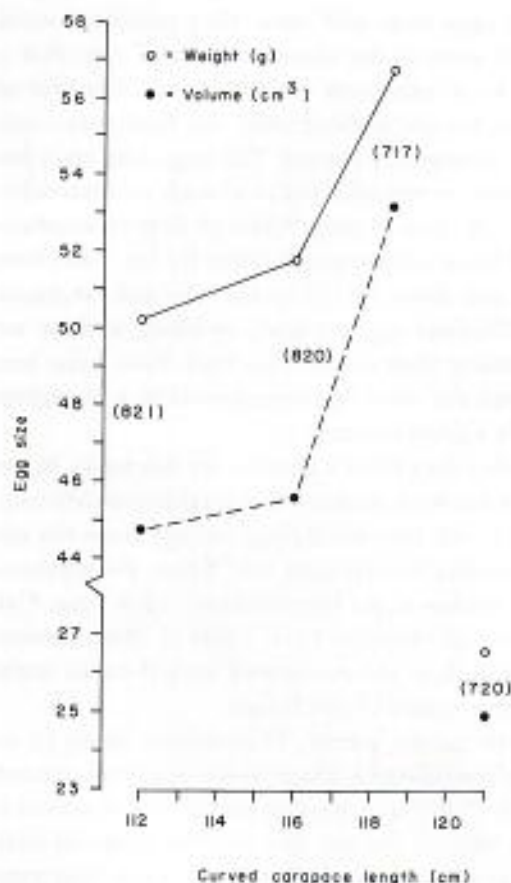
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Figure 31   Relationship between egg size (weight and volume) and curved carapace length in female *Chelonia mydas* (JFCm number indicated in parenthesis) at Mayotte, Comores (see also Table 28).

these one-diameter values could be misleading, for turtle eggs are rarely perfect spheres and are sometimes quite ovoid; more data are needed before sound comparisons can be made. Contrary to Hirth's claim (1971: 3: 7), it was *not* usual to find abnormally small or shaped eggs in the Mohéli clutches: none was encountered in the nine clutches examined.

The case of Mayotte female JFCm 720 is curious; her clutch had the normal number of eggs, but the eggs were half the normal size. This turtle had a stumped left hind limb and asymmetric plastron, and may have been either severly injured as immature, or suffering from congenital malformations. It is difficult to say whether or not the small size of her eggs was directly caused by the injury, or by the nutritional and energetic problems that might result from having a stumped flipper.

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Although these eggs were half-sized, they produced viable embryos. They were, thus, not the same as the abnormally small eggs that occasionally occur in small numbers in an otherwise normal clutch. The few small eggs that appear in normal clutches are without yolk, and hence non-viable.

Incubation and emergence period. Ten eggs laid on 9 June 1972 by JFCm 720 at Moya north were transplanted to a beach on Dzaoudzi and excavated on 6th August by Dr. R. von Hentig. After 58 days of incubation, four eggs had live embryos, and from a photograph taken by Dr. von Hentig, these embryos had external yolk sacs about 1.5 cm in diameter and carapaces about 3 cm long. By 60 days most *Chelonia* eggs are ready to hatch, so these were apparently developing more slowly than usual. This may have been because of low sand temperature and not the small egg sizes; however, a transplanted clutch of half-sized eggs is hardly a good norm.

There are no other data from Comores on this topic. In previous discussions of nesting season it has been assumed that it takes roughly two months from the time eggs are laid to the time hatchlings emerge from the nest. Actual incubation time is presumably several days less. These assumptions are based on the findings of other studies (e.g., Hendrickson, 1958: 504; Carr & Hirth, 1961; Schulz, 1975: 90; see also Frazier, 1971: Table 2). Both Hendrickson and Schulz showed that the length of the emergence period varies with season, probably as a function of temperature of incubation.

Hatching and emergence success. Depressions, about 15 to 20 cm in diameter, with tracks of hatchlings leading to the sea, were recorded on six nesting beaches on Mohéli (Table 9). One emergence was observed on Moya south; at dusk 45 hatchlings entered the sea. Because the Pamanzi beaches were heavily used, it was not possible to find depressions from nest emergences. Clearly, hatchlings are emerging on these beaches, but no other figures are available. Hughes, (1974a: Table 13) gives information on hatching and emergence success from Europa.

One emergence on Chissioua Ouénéfou was witnessed (Table 29) and observations relevant to predation will be discussed in the Predation Section. A behaviour not previously reported in hatchlings was seen in hatchlings that emerged from the nest before the main body of the emergence. The first movements of their flippers were not locomotory as is usual, but resembled the nest digging movements of a female. Several digging strokes were made, with much hesitation, and then the animals began locomoting more rapidly, heading toward the sea. The digging movements may have been attempts by each animal to cover itself with sand and thereby shade itself from direct sunlight (Plate XV). It would appear that the repertoire for nesting behaviour is present in newly emerged *Chelonia* regardless of sex. Thermoregulatory responses in hatchlings of this species have been reported by Bustard (1970: 225), but sand covering of this type has not been reported in hatchlings. Hughes, (1974b: 40)

reported flipper movements that covered the animal with water and moist sand, but this was only reported in nesting females that had been stranded by low tides in the daytime.

Nest Habitat Utilisation

The vast majority of nest pits on Mohéli occur within the first few metres above the beach crest (Figure 32). Nests below this level are very rare: only 5% of all nests with eggs were below the high water mark. At the same time, few nests are made farther than 5 metres inland from the beach crest: 82% of all nests with eggs were between 0 and 5 m inland. No nest pits were found more than 15 m inland. Nesting is concentrated in a narrow zone above the high water mark, but this concentration is as much a reflection of the availability of suitable habitat as a selection on the part of nesting females – nesting habitat simply occurs in narrow strips. There is no difference in the distribution of total numbers of nests with eggs and without eggs [$\chi^2(G) = 21.98$, d.f. $= 20$, p > 0.05].

All nest pits on Mayotte fell between –2 and +8 m from the beach crest, and 91% were from 0 to 5 m (Figure 33). This narrow zone in which nesting occurs is a reflection of the widths of beaches available; the vast majority are less than 10 m wide. Nest pits thought to have eggs rarely occurred below the beach crest; less than 2% were in this category. More than 13% of nest pits without eggs were below the beach crest; the distributions of nest pits with and without eggs are different [$\chi^2(G) = 50.06$, d.f. $= 11$, p < 0.001].

On both Mohéli and Mayotte, nesting beaches are narrow, and considering just nests with eggs, nesting on Mohéli is slightly more inland from the beach crest. This difference is statistically significant [$X^2(G) = 49.24$, d.f. $= 116$, p < 0.001]. However, a higher proportion of nestings on Mayotte seems to be successful: 54% of all Mayotte nests were scored as successful while only 48% of those on Mohéli were with eggs; the difference is highly significant [$\chi^2(G) = 34.46$, d.f. $= 2$, p < 0.001]. If only nests that could be scored as either with or without eggs are included, the proportions of successful nesting for Mayotte and Mohéli are 67% and 55%, respectively. Again, the difference is highly significant [$\chi^2(G) = 18.16$, d.f. $= 1$, p < 0.001]. The higher nesting success on Mayotte may be related to the greater degree of overcrowding by turtles on Mohéli.

There are several lines of evidence, besides general impressions, that these narrow beaches are being overcrowded during peak nesting. The proportion of nest pits thought *not* to contain eggs increases as nesting activity increases from February/March/April to June (Figure 34). This was not true on beach 24, a small beach with very little nesting and nests well spaced out. And, it is not certain on beach 47, but if the incomplete February count – representing about
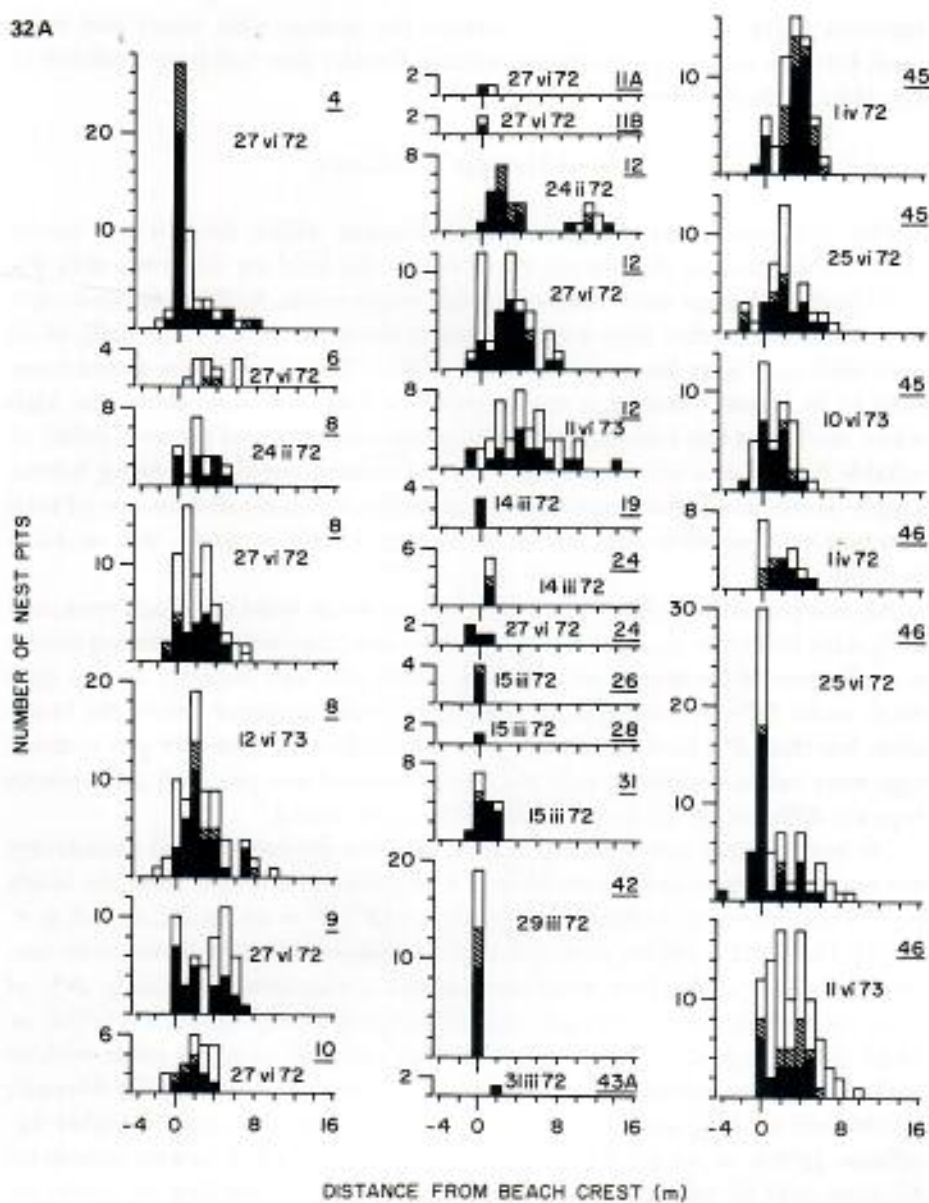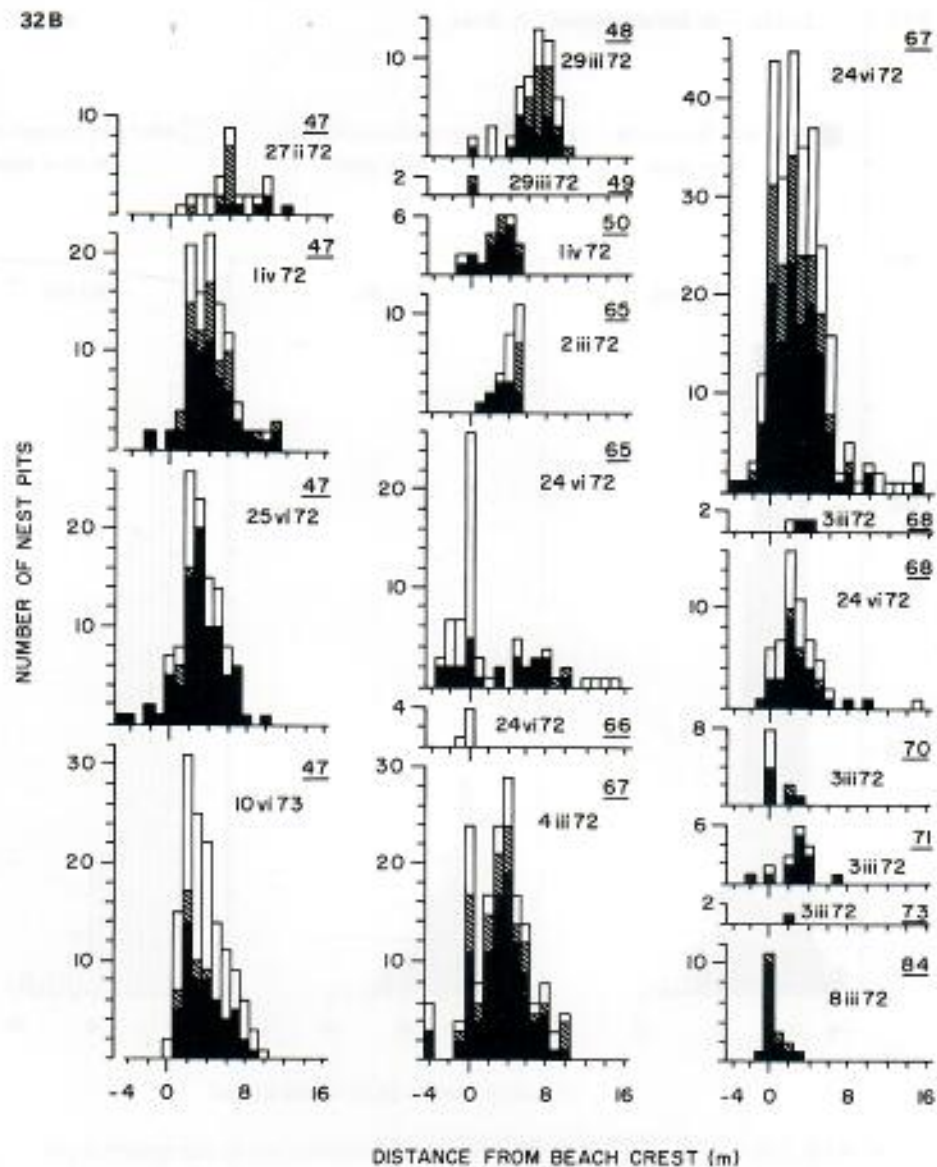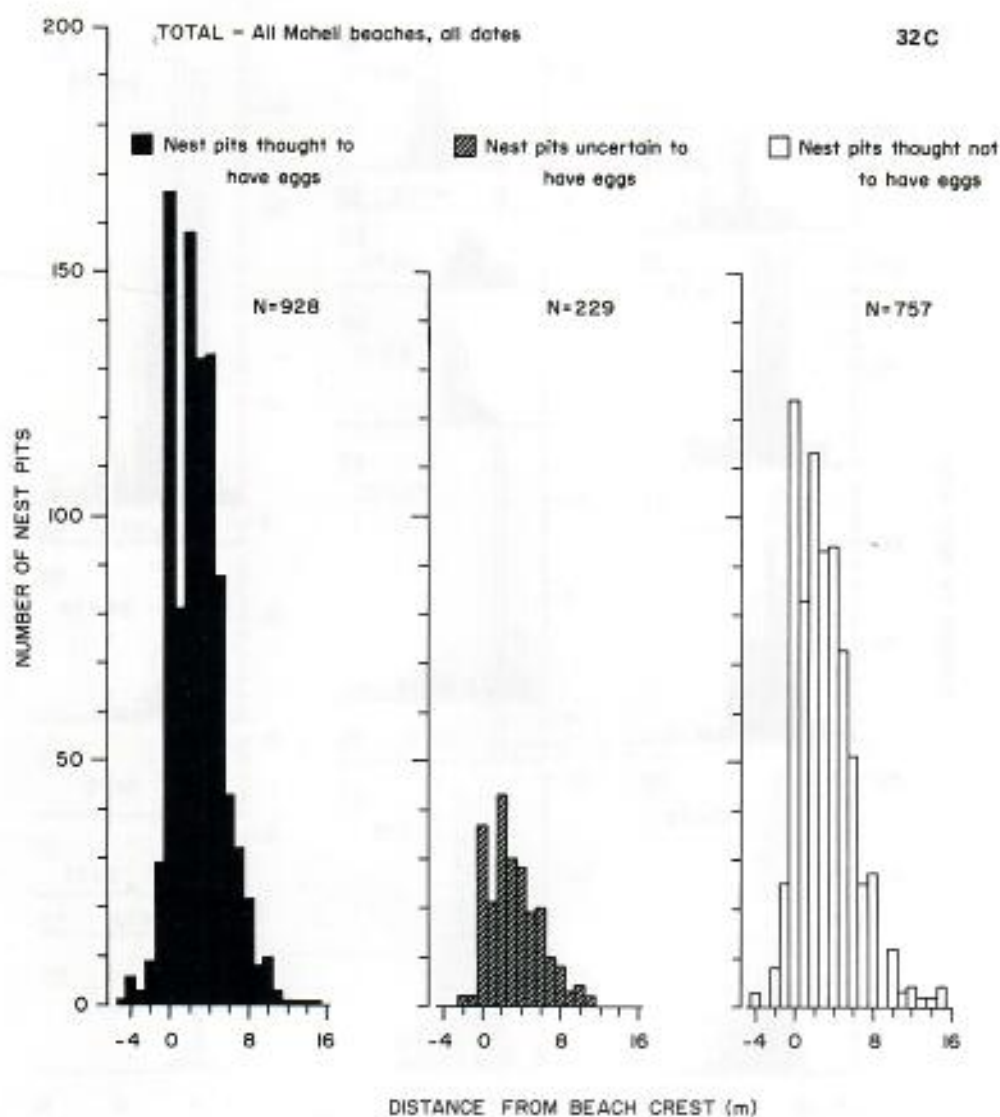
Figure 32   Distance from beach crest distributions of *Chelonia mydas* nest pits from 29 beaches at Mohéli, Comores; A & B – beach number and date of observation are indicated; nine beaches with more than one date of observation; C – total (see also Tables 9 & 11).

NUMBER OF NEST PITS

DISTANCE FROM BEACH CREST (m)

TOTAL – All Moheli beaches, all dates

32C

■ Nest pits thought to have eggs   ▨ Nest pits uncertain to have eggs   □ Nest pits thought not to have eggs

NUMBER OF NEST PITS

N=928   N=229   N=757

DISTANCE FROM BEACH CREST (m)

1/10 of the beach – is rejected, then this beach also conforms to the general pattern.

The number of sites of egg shells exposed on these beaches also increases as the nesting season progresses (Table 30). Beach 24 had none exposed at any time, but this beach had very little nesting. Beach 67 had nine sites of egg shells in March and eight in June. However, all nine March sites had been exposed by dogs' digging, whereas, only one of the eight June sites had obviously been exposed by dogs. Exposure of egg shells (and buried eggs) is often due to females digging up nests during their own nesting efforts.

Increased nesting activity aggravates the disturbance to the sand, decreasing moisture content. This results in poorer sand conditions and reduces the chances of a successful nest being made. The net effect is more abortive attempts before successful nesting, which further aerates the sand and reduces the quality of the nesting habitat. The system quickly becomes a positive feedback loop, and the chances of digging up a previously made nest are greatly increased (cf. Bustard & Tognetti, 1969; Frazier, 1980a: 232 ff.).

The main nesting zone moves toward the sea as the season progresses (Table 31), with the modal nesting zone shifting from between 2 to 4 m inland of the beach crest to between 0 and 2 metres. Seasonal changes in beaches could explain such shifts in nesting if erosion were cutting the beach crest farther inland. This phenomenon could not, however, explain the situation reported here, for most of the nest pits had been recently dug and their positions relative to the beach crest were very similar to when the respective females nested. This is not to say that some nest pits were never recounted on subsequent visits – certainly some were. Furthermore, the Mohéli beaches appeared to be relatively stable and did not undergo large enough changes to account for these shifts in modal nesting zone. It seems rather that the females are nesting closer to the sea during peak nesting. The sand closer to the beach crest may be moister and less friable than that inland, and this would make it advantageous to nest closer to the sea.

The Pamanzi beaches also appeared overcrowded, for there was considerable nesting activity concetrated in very narrow areas. Excluding nest pits uncertain to have eggs, nearly 52% of the nest pits in Pamanzi were scored as without eggs, while only 13% of nest pits on other beaches were without eggs. This difference is highly significant [$\chi^2(G) = 61.58$, d.f. $= 1$, p < 0.001], and is further evidence that these beaches are being so heavily disturbed by nesting turtles that many nesting efforts were unsuccessful – a symptom of an overcrowded beach (cf. Bustard & Tognetti, 1969; Frazier, 1980a: 232 ff.).

Eretmochelys imbricata (Linnnaeus)

The significance of the *Eretmochelys* population at Comores has doubtless been overshadowed by the Archipelago's proximity to and historic ties with Madagascar and the much greater turtle populations at that island. Furthermore, the difficulty in assessing the status of a population of this species leaves many very basic questions unanswered.

Common Names in Use

Throughout the Comores this turtle is known as 'Nyamba'; Gevrey (1870: 115) recorded 'Namba' for all turtles, and Mr. A. Malida, a schoolboy at Nioumachoua, Mohéli, reported 'Gnamba.' The turtle is known more specifically as

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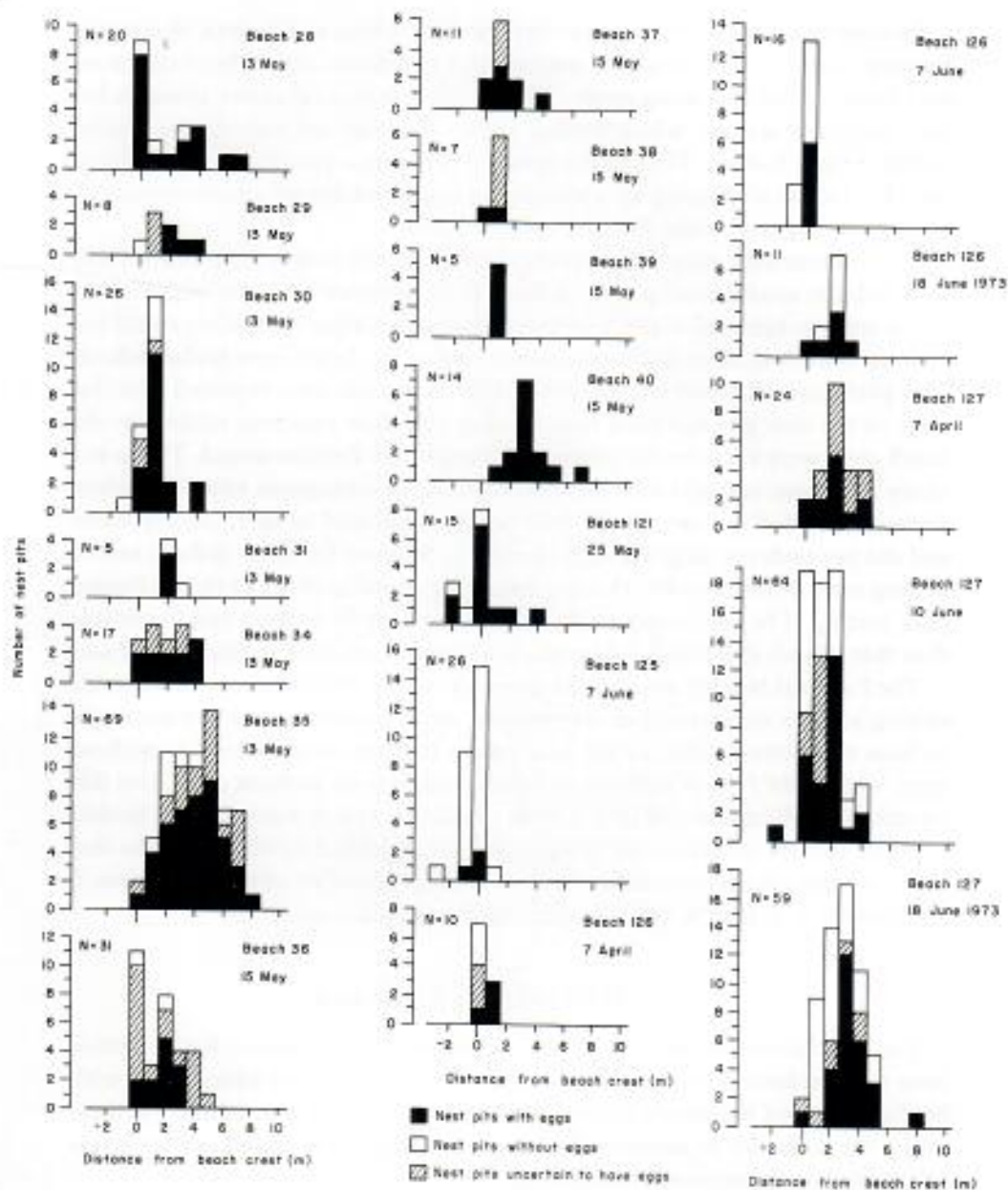
33 A

Figure 33   Distance from beach crest distributions of *Chelonia mydas* nest pits from 15 beaches at Mayotte, A – beach number and date of observation are indicated, three beaches with more than one observation; B – total (see also Tables 13, 14 & 15).
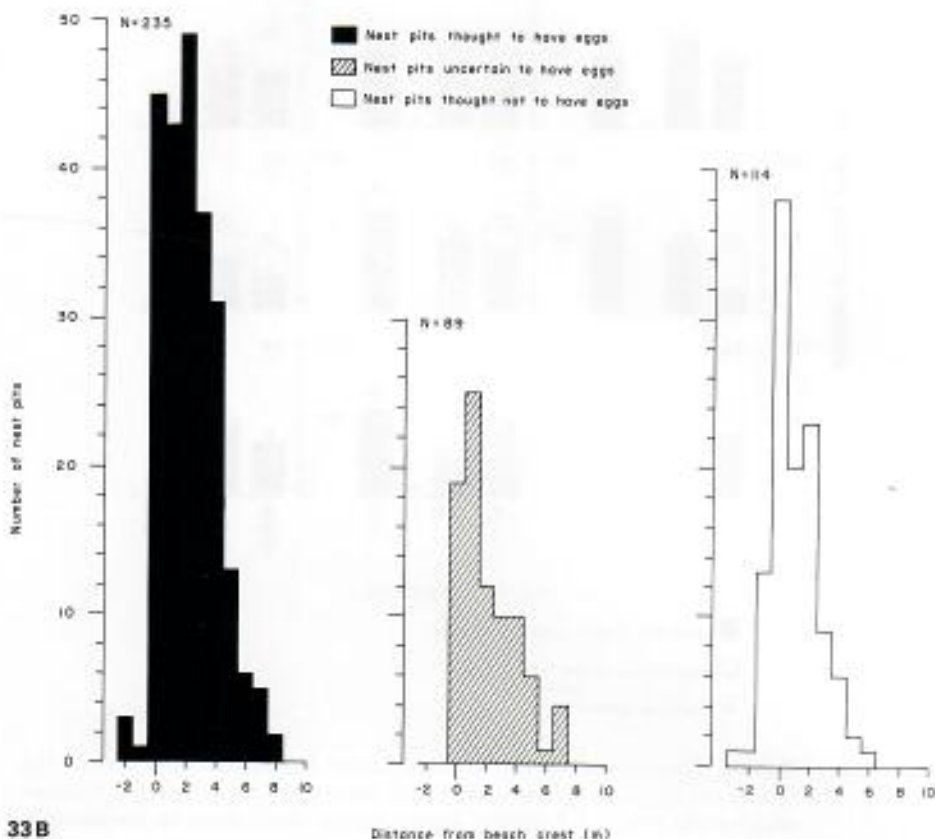
33 B

Distance from beach crest (m)

'Nyamba Malé,' which translates as 'Money turtle,' for this is the turtle of trade. On the Swahili-speaking coast of eastern Africa, from southern Somalia to northern Mozambique, this species is referred to as 'Ng'amba' and this name is clearly related to the Comorian name. In Swahili, 'gamba' means 'scale,' and it is probably from this word that the name 'Ng'amba' is derived. 'Fanu' is a general name for marine turtles used in Madagascar; on Mayotte it was used for *Chelonia*, but it might also be used for *Eretmochelys*. French names, common throughout the region, are 'Caret' and 'Tortue d' écaille.' The common English name is 'Hawksbill Turtle.'

Occurrence

Eretmochelys is evidently resident at all the Comoro Islands, which will be dealt with individually, as their respective populations are thought to be separate (see Section on Movements and Migrations).
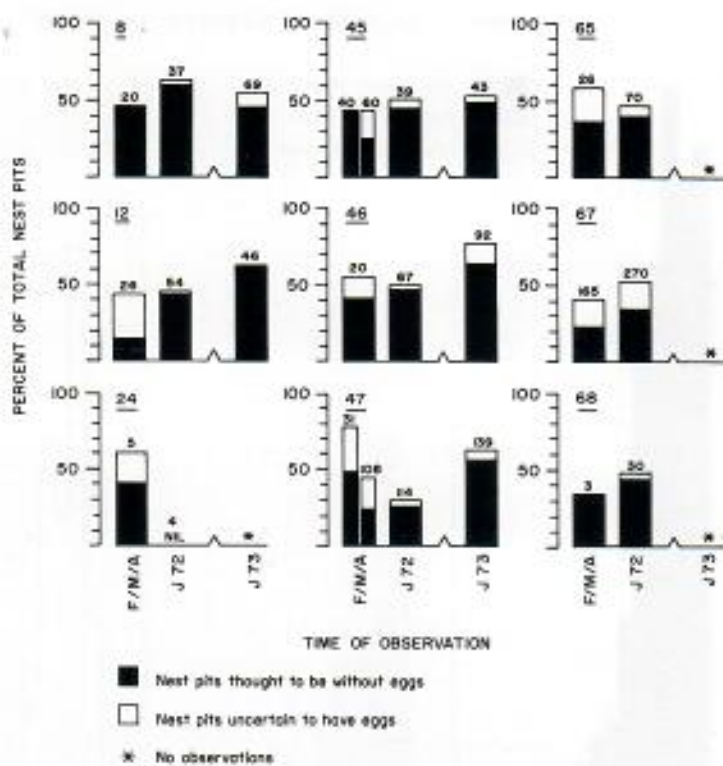
Figure 34   Seasonal change in percent of *Chelonia mydas* nest pits thought to be without eggs (black) and uncertain to have eggs (white), from 9 beaches on Mohéli, Comores; observations: F/M/A = February/ March/ April (2 observations for this period for beaches 45 and 47, February observations on beach 47 represent about 1/10 of the beach); J 72 = June 1972; J 73 = June 1973; figure above each bar is the total number of nest pits for that observation (see also Table 31).

At Grande Comore, there are records from: south of Choua–Chandroudé, in the northeast; Mitsamiouli, in the northwest; Itsandra, Moroni and Iconi in the west; and Malé in the southeast. As there are records from the five months of the year when observations were being made, it is likely that the species occurs throughout the year (Tables 32 & 33).

At Mohéli this turtle was recorded at the offshore islands in the south and at the east and northwest of the main island (Tables 32 & 33). Nesting spoor was observed on at least 14 beaches extending from the southwest to the northeast (Table 34). Records occurred from late February until late June, and the species is suspected to be present also during the second half of the year, when no observer was present.

There is but one record at Anjouan, from the northwest in June. Although

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the species may not be common here, it is suspected to occur generally around the island and throughout the year.

At Mayotte single turtles were seen in shallow water in the northeast, east, south and west of Mayotte, in May and June. Nesting spoor was on four beaches, in the northeast, east and southeast, and bones of this turtle were also seen on beaches in the north (Table 4). The species is probably resident throughout the year, and with the vast areas of reef that encircle the Island, it must occur widely.

Eretmochelys was recorded most frequently at Grande Comore, but there was much more nesting activity at Mohéli; the species is probably more common at Mayotte and Mohéli.

Population Size and Structure

At Grande Comore all of the animals measured and observed were immatures (Tables 32 & 33; see Section on Morphometrics). There is evidently a small, perhaps moderate, population at this island. Breeding is not recorded, and the adult population, if it occurs, must be small.

At Mohéli, immatures were recorded, but fewer were observed than at Grande Comore where the larger and more affluent human population would buy trophies as they became available, making it more likely to see them. Mr. A. Malida, in answering a questionnaire on turtles, wrote that the species is not hunted much at Mohéli because the flesh is poisonous and the animal is of little value to the fishermen. The immature population at Mohéli, with the greater area of reef and shallow water, is expected to be much larger than the data suggest.

Nesting spoor was recorded on at least 14 beaches around Mohéli. The amount of nesting spoor recorded indicates a small population, but the main nesting period may not have been observed, and *Eretmochelys* spoor is ephemeral – even fresh it is often inconspicuous. Nevertheless, the annual nesting population is probably well below 50.

Too little is known from Anjouan to speculate; both immature and adult populations would appear to be small.

At Mayotte all of the live animals seen were smaller than adults, but nesting occurs, and several dead adult specimens were seen on nesting beaches. Adults and immatures of both sexes probably occur, but immatures seem to be more common. Nesting spoor was confirmed on only three beaches, and three nests with eggs were recorded. The annual nesting population of *Eretmochelys* at Mayotte is certainly greater than three, but dispersed and ephemeral nests of this turtle serve as poor indicators of population size.

Movements and Migrations

Little is known about the migrations of *Eretmochelys*, and there is no direct evidence from Comores. None of the four animals tagged and released have been reported recaptured (Table 33). Mayotte probably has a resident population, and the quantity of rich, live reef at this island may serve as important feeding habitat for turtles that nest at other islands in the Archipelago.

Movements of up to 27 km have been recorded in the archipelago system of Seychelles (Diamond, 1976: 208). Carr, Hirth & Ogren, (1966: Table 5) reported movements from the Tortuguero, Costa Rica, rookery of up to 325 mi. (= 523 km, erroneously converted in Carr & Stancyk, 1975: Table 3, to 463 km). The species is obviously capable of long distance movements and could arrive at either side of the Mozambique Channel having started from Comores. There is, however, a suggestion that *Eretmochelys* is more sedentary than is *Chelonia* (cf. Carr & Stancyk, 1975: 167). While movements among islands in the Archipelago, and to and from the Archipelago, probably do occur, it seems likely that each island has its own population.

Morphometrics

Immatures. The nine animals measured at Grande Comore ranged from 34.0 to 67.0 cm in curved carapace length, and three specimens from Mohéli and one from Anjouan fell within this range (Figure 35). The grand average was 44.03 m ($\pm$ 2.658). The smallest *Eretmochelys* reported nesting on Cousin Island, Seychelles was 83.0 cm in curved carapace length (Diamond, 1976: 202), and the smallest nesting female found on Maziwi Island, Tanzania, was 87.0 cm in curved carapace length (Frazier, unpublished data). There is little question that all of the Comoro aninals reported here are immatures.

Carapace width measurements ranged from 29.5 to 58.0 cm, averaging 38.82 ($\pm$ 2.149). Plastron lengths varied from 25.5 to 50.0, with an average of 33.37 ($\pm$ 2.403). Head widths ranged from 5.2 to 9.0, averaging 6.45 ($\pm$ 0.456) (Figure 35). The size-frequency distributions for each of these variables have distinct modes at the lower ends of the respective size ranges. Evidently a preponderance of small animals are being caught, possibly because they are the largest part of the population.

Carapace width increases with carapace length. The relationship appears isometric, for the slope of the regression line of the log log transformed data (0.90562) is not significantly different from the isometric line ($t = -1.84$, d.f. $= 11$, $p > 0.05$).

Plastron length also appears to be related to carapace length in an isometric way. The slope of the log log plot is 1.06817, not significantly different from 1 ($t = 1.80$, d.f. $= 9$, $p > 0.1$).

Head width shows a relationship that is also approximately isometric. The slope of the log log transformed data (0.86528) is not significantly different from 1 (t = −1.86, d.f. = 6, p > 0.1).

The failure of these t-tests to show significant differences between the log log transformed data and the isometric line may be related to the small sample sizes involved, rather than the presence of a true isometric relationship. Analysis of morphometric relationships of a larger range of animals indicate that allometric changes are occurring (see Section on Size Comparisons).

Hatchlings. A sample of eight hatchlings caught and killed by *Ocypode* sp. on 26 February, 1972, at Chissioua Ouénéfou, Mohéli were collected and measured. They are all assumed to have emerged from the same nest on beach N° 47. Weights two days after emergence ranged from 11 to 13.5 g, averaging 12.62 (± 1.070). Because these were not recorded immediately after emergence, weights are likely to be about 1 or 2 g light (cf. Frazier, 1971: 383).

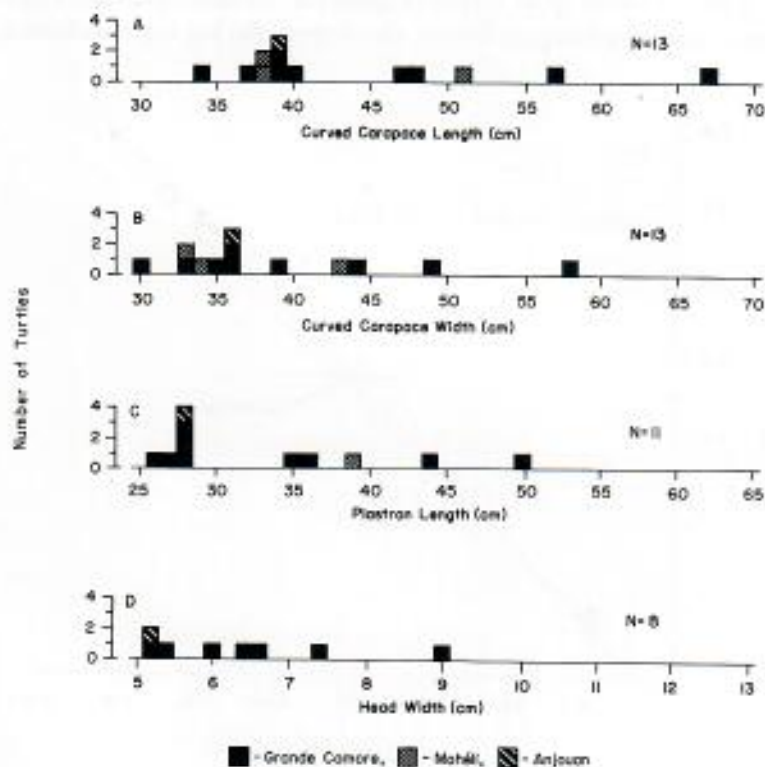Carapace lengths varied from 39 to 43 cm, a range of almost 10% of the

Figure 35   Size-frequency distributions of body measurements of *Eretmochelys imbricata* at Comores: A – Curved carapace length; B – Curved carapace width; C – Plastron length; D – Head width; N ranges from 8 to 13 (see Table 33).

mean, 41.10 (± 1.036). Carapace widths varied from 30 to 33 cm, again nearly 10% of the average, 32.30 (± 1.033). Plastron lengths ranged from 31 to 35 cm (33.72 ± 1.043). Head widths varied from 14 to 15.5 cm (14.74 ± 1.045). There was no significant relationship between weight and carapace length in these hatchlings (r = 0.20023, d.f. = 6, p > 0.1), and no significant relationships between carapace width and carapace length (r = 0.15103, d.f. = 6, p > 0.1) or head width and carapace length (r = 0.39610, d.f. = 6, p > 0.1). Plastron length and carapace length are strongly related (r = 0.72707, d.f. = 6, p < 0.05). Small sample sizes may account for the lack of significant correlations.

Size Comparisons

Plotting measurements of immatures together with hatchlings of *Eretmochelys* reveals morphometric trends not evident in analyses of these data separately. Carapace width increases relative to carapace length; the slope of the log log transformed data is 1.04741, which is significantly greater than the isometric line (t = 5.56, d.f. = 21, p < 0.001) (Figure 36). Relative plastron length decreases with increasing carapace length; the slope of the log log transfomed data
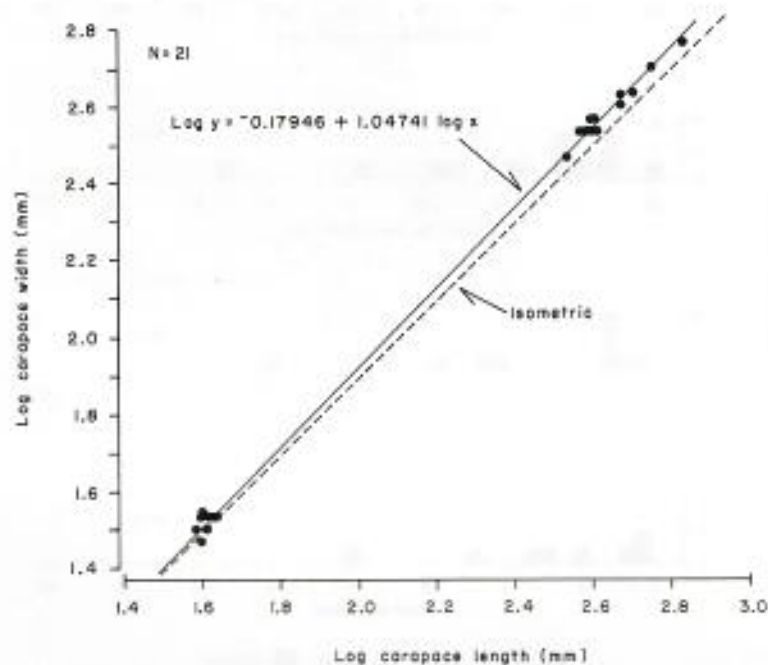

Figure 36   Relationship between log curved carapace width and log curved carapace length in hatchling and immature *Eretmochelys imbricata* at Comores; showing least squares fitted line and theoretical isometric line.

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is 0.95616, significantly less than 1 (t = −7.08, d.f. = 17, p < 0.001) (Figure 37). Head width shows a dramatic allometric reduction, the regression line of the log log transformed data has a slope of only 0.60931, considerably less than the isometric line (t = −25.79, d.f. = 01, p < 0.001) (Figure 38).

These trends are the same as those seen earlier for *Chelonia*. As hatchlings increase in size to immatures, the carapaces get relatively wider, the plastrons get relatively shorter and the heads, relatively narrower.

Scalation

Immatures. Lepidosis in the immatures was typical of the species; in 12 cases the carapace was unvarying in having five vertebrals, four pairs of pleurals, and 11 pairs of marginals, in addition to a single cervical and pair of supracaudals. In 10 of these specimens there was no variation from the normal six pairs of plastron scales, and the intergular was always conspicuous in size. Inframarginals were a constant four per side. Axillaries were variable with two pair, three pair and asymmetric combinations of two and three scales per side. Inguinals were usually one per side, but cases with none or two on a side were each recorded once. The postanal varied from small to moderate in size. Eight animals
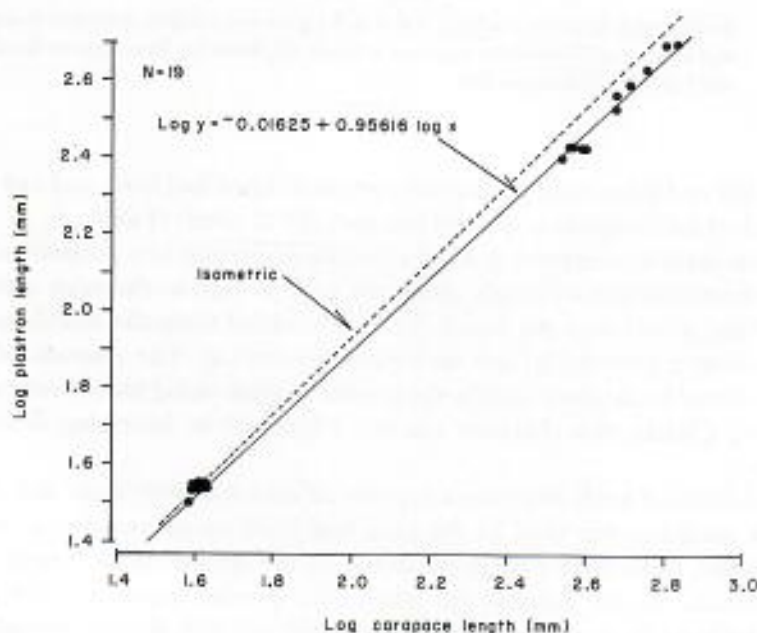

Figure 37   Relationship between log plastron length and log curved carapace length in hatchling and immature *Eretmochelys imbricata* at Comores; showing least squares fitted line and theoretical isometric line.
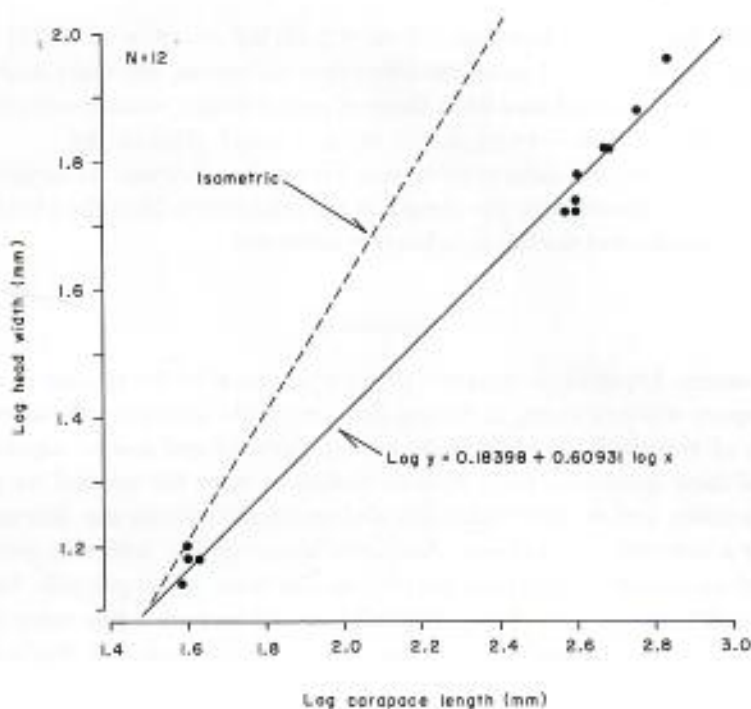
Figure 38   Relationship between log head width and log curved carapace length in hatchling and immature *Eretmochelys imbricata* at Comores; showing least squares fitted line and theoretical isometric line.

had three left and three right postoculars; one individual had three and one half on each side (two complete scales and one partially divided) (Table 33).

The most anterior marginal to form a dentate projection was determined by passing a vertical pencil anteriorly along the edge of shell to the most anterior marginal that would stop the pencil. This scale varied from the fourth to the eighth, counting posteriorly, not including the cervical. The position of the scale was related to carapace length, the smaller animals being more denticulate (Figure 39). Clearly, this character can be of little use in describing different populations.

The condition of keels also shows a strong relationship with body size. Animals with carapaces less than 40 cm long had keels on all vertebrals. In the smaller turtles, these were very pronounced on the second, third, fourth, and fifth vertebrals. As the animals get larger, the anterior scales had less pronounced keels, to the point where only the fourth and fifth showed prominent ridges. The first vertebral may actually lack any sign of a keel in animals with curved carapace lengths of 40 cm or longer (Figure 40).

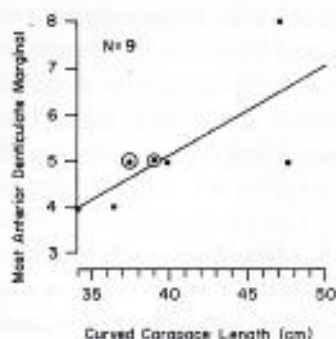Keels occured on all pleurals in smaller animals, and they were prominent on

Figure 39   Relationship between the most anterior denticulate marginal and curved carapace length in immature *Eretmochelys imbricata* at Comores; least squares fitted line is y = 0.18480x − 2.24173; r = 0.72194, d.f. = 7, p < 0.05.

the second, third, and fourth. In larger animals only the posterior keels were prominent, and in some cases the anterior pleurals had no traces of keels.

Plastron keels showed a similar phenomenon. Prominent ridges ran anterio-posterior and from the humerals to the anals on both sides of the midline. In the larger specimens, 47.0 and 47.5 cm in curved carapace length, the keels on the humerals were absent (Plates XVI and XVII: Figure 1).

Keel characteristics were thought by Agassiz (1857: I, 382), and also Carr, 1952: 377), to be distinctive of major races: the Indo-Pacific was reported to
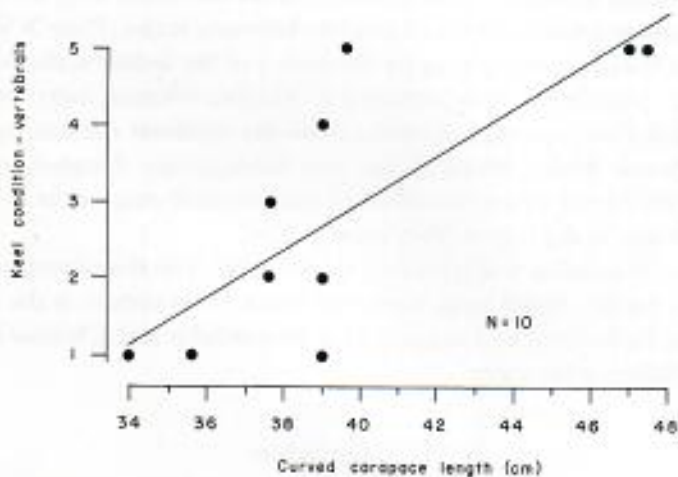

Figure 40   Relationship between condition of vertebral keels and curved carapace length in immature *Eretmochelys imbricata* at Comores: 1 – all with strong keels; 2 = all with keels, strong on 2nd to 5th; 3 = all with keels, strong on 3rd to 5th; 4 = all with keels, strong on 4th to 5th; 5 = keels on 2nd to 5th; least squares fitted line: y = 0.31011x − 9.41434, r = 0.77209, d.f. = 8, p < 0.01.

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have more prominent keels in both carapace and plastron. Specimens from Aldabra (Frazier, 1971: 399), and Comores do not conform to Agassiz' description in regard to keels, and since the condition of this character is dependent on the size (and age?) of the animal, it is of little use in distinguishing populations.

Hatchlings. Those measured had typical scalation: they all had normal carapaces and plastrons; the intergular was large in all cases. Six animals each had four pairs of inframarginals and two other turtles each had three scales on one side and four on another. Six hatchlings each had three pair of axillary scales, and two other individuals each had two scales on one side and three on another. One pair of inguinals occurred in each of six turtles, and two other animals each had one scale on one side and two on the other. One hatchling was atypical in each instance, but the atypical condition was shared by three other individuals for each of the three scale types. Six hatchlings each had three pairs of postoculars. The postanal was of moderate size in five, and large in three hatchlings.

There were conspicuous keels on all pleurals. Neither the vertebrals nor the plastron were keeled.

Coloration

In all 10 immatures examined, plastron colour was yellow (Table 33). Seven animals had black centres to the intergulars and one specimen had two black spots in this scale. All eight of these animals had black centres to the scales in the axillary and inguinal areas. The carapace scutes were dark, mottled with grey, yellow and off-white. Dorsal scales of head and limbs were all black, outlined by light-coloured sutures or borders between scales (Plate XVII: Figure 2). This last feature is thought to be distinctive of the Indo-Pacific populations (Carr, 1952: 366). It has been reported at Aldabra (Frazier, 1971: 399), but is evidently not always present in turtles from the southern African region (Republic of South Africa, Mozambique and Madagascar) (Hughes, 1974a: 18). Animals with 'blond' or cream-coloured tortoise-shell may occur in Comores, but as elsewhere in the region, they must be rare.

Hatchling coloration was typical of *Eretmochelys*. The dorsal surface was reddish-brown while ventral parts were mat black. This pattern is the reverse of pelagic countershading, and suggests that *Eretmochelys* and *Chelonia* hatchlings have very different life styles.

Feeding habits

A preliminary analysis of the stomach contents of JFEi 21, an immature from Moihani, showed four types of sponges (Class Demospongea): *Aaptos* sp. and *Tethya* sp. (Tethyidae), *Amphimedon* sp. or *Niphates* sp. (Niphatidae) and *Stelletta* sp. (Stellettidae) (K. Ruetzler, pers. com.). These findings are consistent with