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SAST - Green turtle - 5,31 (07) 005,02

SYNOPSIS OF BIOLOGICAL DATA ON THE GREEN TURTLE
Chelonia mydas (Linnaeus) 1758

Prepared by
H.F. Hirth

FOOD AND AGRICULTURE OGANIZATION OF THE UNITED NATIONS
ROME, 1971

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- SAST Data concerning certain species and fish stocks.
- MAST Information on methods and subjects.
- OT Oceanographic data.
- IT Limnological data.

and

- CART Information concerning fisheries and resources of certain countries and regions (FID/S).

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- SAST Données sur certaines espèces et populations de poissons.
- MAST Renseignements sur des méthodes et des sujets.
- OT Données océanographiques.
- IT Données limnologiques.

et

- CART Renseignements sur les pêcheries et les ressources de certains pays et régions (FID/S).

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y

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- RE Indexed lists of experts and institutions drawn from Registers maintained by the Fishery Resources Division.
- CB Lists of periodicals, special sections of " Aquatic Sciences and Fisheries Abstracts (ASFA), " special bibliographies and papers concerning documentation problems.
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- RE Listes indexées d'experts et institutions tirées des registres tenus à jour par la Division des ressources halieutiques.
- CB Listes de périodiques, des sections spéciales de la « Aquatic Sciences and Fisheries Abstracts (ASFA) », des bibliographies particulières et des articles sur les problèmes de documentation.
- MFS Editions provisoires des « Manuels FAO de science halieutique ».

Grupos especiales de documentos técnicos se identifican por las siglas siguientes:

- RE Listas índices de expertos y de instituciones tomadas de los registros que se llevan en la Dirección de Recursos Pesqueros.
- CB Listas de periódicos, secciones especiales de la « Aquatic Sciences and Fisheries Abstracts (ASFA) », bibliografías especiales y trabajos relativos a los problemas de documentación.
- MFS Ediciones provisionales de los « Manuales de la FAO de Ciencias Pesqueras ».

Some documents also have another identification, if, for example, they have been contributed to a meeting for which papers have been numbered according to another system.

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SYNOPSIS OF BIOLOGICAL DATA ON THE GREEN TURTLE

Chelonia mydas (Linnaeus) 1758

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Rome, December 1971

PREPARATION OF THIS SYNOPSIS

The present document which is the first FAO Species Synopsis on biological data of commercially important marine turtles, has been prepared following the annotated outline for species synopsis of data on species and stocks (FAO Fisheries Synopsis No.1 Revision 1, 1965), modified by the author to meet the special requirements of a synoptic review of turtle species.

The main purpose of this synopsis is to bring together the current information on the natural history of the green turtle, Chelonia mydas, and to draw attention to the major gaps in our knowledge of the species. In a few sections some of the older, classical papers are cited and summarized in order to make the synopsis more comprehensive.

The author is indebted to Mrs. Joan Hubbard, Interlibrary Loan Librarian and Mrs. Jeanne Chapin, Life Science Librarian, University of Utah, for their help in tracking down rare manuscripts; and to Dr. John Hendrickson (University of Arizona) for allowing the author to peruse his personal library. Mrs. Kennie Harris, Mrs. Bess Short and Miss Liwana Blau graciously and conscientiously typed several versions of the manuscript. The University of Utah Library and the Department of Biology financially aided the work through the purchase of interlibrary loans.

Dr. Archie Carr (University of Florida) and Dr. H. Robert Bustard (The Australian National University) offered helpful suggestions after critically reading the manuscript and to them the author is indebted.

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C O N T E N T S

*As no information was available to the author, this item has been omitted from the text

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Chelonia mydas (Linnaeus) 1758

1.12 Objective synonymy

Testudo mydas Linnaeus, 1758, p. 197, Syst. Nat. (Ed. 10) Stockholm. Type locality, Ascension Island.

Chelonia mydas Brongniart, 1800, Bull. Sci. Soc. Philom., 2:89

Some authors consider the generic designation by Brongniart a nomen nudum. For example, Deraniyagala (1939) recognizes the following:

Chelonia mydas Latreille, 1802, Hist. Nat. Rept. i, p. 22

1.2 Taxonomy

1.21 Affinities

- Suprageneric

Kingdom Animalia
  Subkingdom Metazoa
    Phylum Chordata
      Subphylum Vertebrata
        Superclass Tetrapoda
          Class Reptilia
            Subclass Anapsida
              Order Testudinata
                Suborder Cryptodira
                  Superfamily Chelonioidea
                    Family Cheloniidae

- Generic

Chelonia Brongniart, Bull. Sci. Soc. Philom. Vol. 2, 1800, p. 89. Genotype: Testudo mydas Linnaeus.

The following generic identity is given by Carr (1952): "One pair of prefrontal scales; tomium of lower jaw coarsely toothed, that of the upper jaw with strong ridges on its inner surface; lateral laminae, 4." Longer descriptions can be found in Deraniyagala (1939), Smith and Taylor (1950) and Loveridge and Williams (1957).

- Specific

Chelonia mydas is easily differentiated from its congener, the flatback turtle, Chelonia depressa Garman, by its more highly arched carapace, sloping marginals and large scales in the middle of the front flippers (Fig. 1). In contrast, C. depressa has a depressed carapace, upward-curving marginals and small scales in the middle of the front flippers. Further differences between the two species are pointed out by Williams, Grandison and Carr (1967), Bustard (1969b), Bustard and Limpus (1969), and Cogger and Lindner (1969).

1.22 Taxonomic status and definition of size categories

The green turtle is a morpho-species. Because size categories of marine turtles are not standardized, the four categories used in this report are defined as follows: hatchling = still bearing conspicuous umbilical scar; first few weeks of post-hatching life; juvenile = umbilical scar inconspicuous or absent and carapace length up to 40 cm (40 cm is about one-half the carapace length of a reproductively mature individual); sub-adult = post-juvenile but not yet reproductively mature (carapace length 40 to 80 cm); adult = reproductively mature; carapace length greater than 80 cm (the minimal size at which females lay eggs is about 80 cm; for convenience it is assumed that males mature at about the same time). Carapace lengths are straight-line distances. A "yearling" is a one-year-old turtle.

1.23 Subspecies

It is best to use the binomial, Chelonia mydas, for all green turtles until a detailed taxonomic study is made. However, several subspecies have been described, and no doubt other races will be named in the future. In fact, the mydas complex may be one circumglobal "Rassenkreis" but with significant gaps between the eastern Pacific and western Atlantic-Caribbean populations and between the East African and West African populations. Subspecific names have been based largely on coloration, although Smith and Taylor (1950) state that a common arrangement restricts mydas to the Atlantic and agassizii to the Pacific Ocean either as species or subspecies. At least some of the subspecific terminology has been perpetuated in checklists and guidebooks by Schmidt (1953), Conant et al. (1956), Conant (1958), Fukada (1965), Stebbins (1966) and Keiser and Wilson (1969), among others.

The Atlantic green turtle, Chelonia mydas mydas (Linnaeus) is found in the Atlantic Ocean, Caribbean Sea, Gulf of Mexico and the Mediterranean Sea. It has a predominantly brownish carapace, sometimes with olive or dark brown blotches and streaks, and the dorsal surfaces of the head, flippers and tail are also predominantly brownish. The spaces between the scales on the top and sides of the head are yellowish; the plastron is usually whitish. The shell of the male is more elongate than that of the female. A detailed description of the subspecies can be found in Carr (1952).

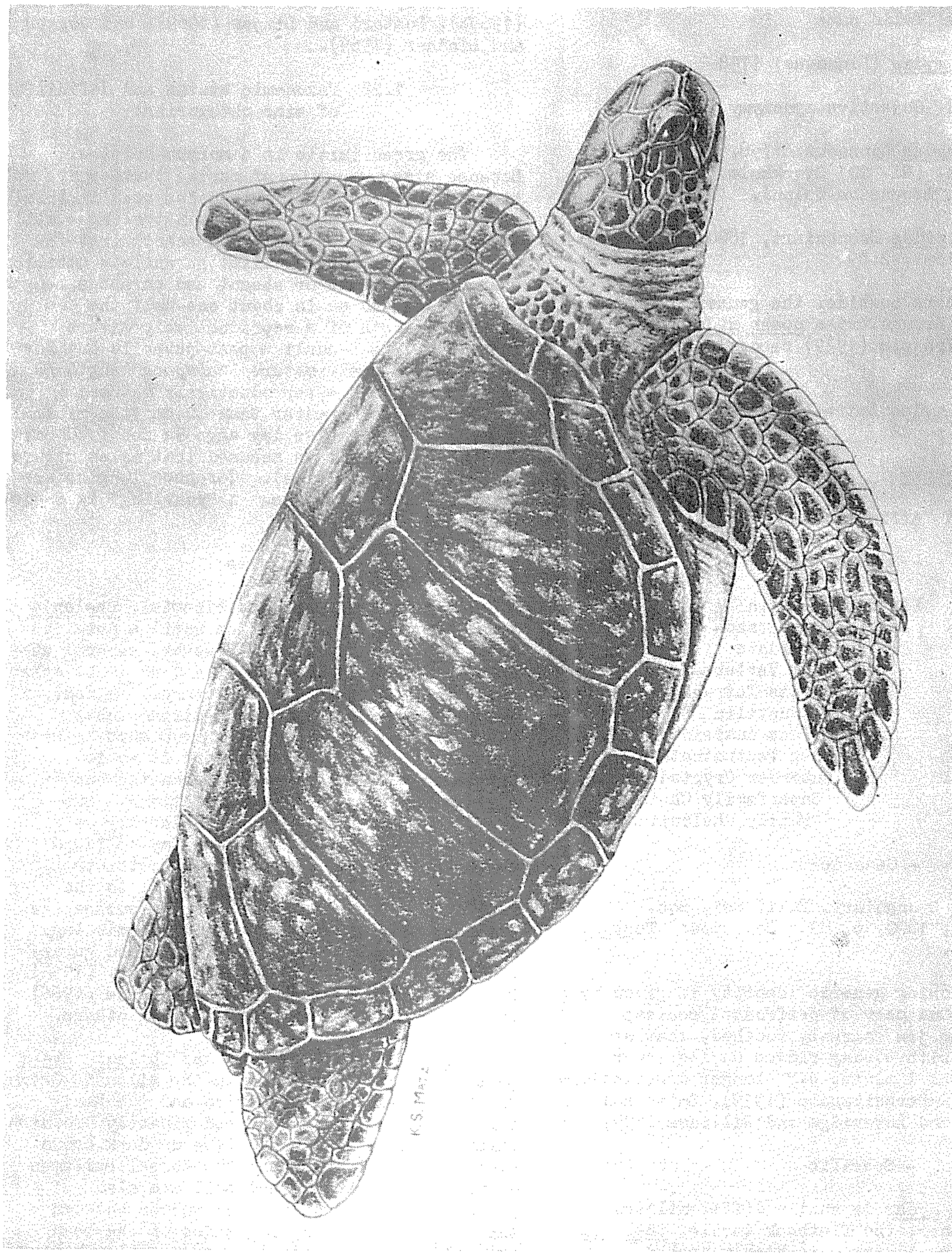

Fig. 1 An adult, female green turtle, Chelonia mydas, from the Gulf of Aden. The green turtle has been called the world's most valuable reptire (drawing by K.S. Matz)

Compared to the Caribbean population, adult females in the Ascension Island population have a more angular emargination of the shell over the neck (Carr and Hirth, 1962).

The East Pacific green turtle, Chelonia mydas agassizii Bocourt, is found along the Pacific coasts of Central and South America. The carapace is basically greenish or olive-brown but sometimes strongly flecked with black, and generally more highly arched and narrower than that of an Atlantic green turtle. The carapace is sometimes markedly indented above the hind flippers - this is usually lacking in individuals from the Atlantic (Carr, 1952). Much earlier, Baur (1890) stated "there is no doubt whatever that the Chelonia from the Pacific is a different species from the Atlantic; the skulls are the same, but there are great differences in the form of the carapace".

One of the most easily recognizable forms in the entire mydas complex is the Northeastern Pacific green turtle, Chelonia mydas carrinegra Caldwell. This subspecies is characterized by black pigmentation on both dorsal and ventral surfaces. The carapace is highly arched in large females while it is low in large males. It occurs in large numbers throughout the Gulf of California and on the outer coast of Baja California. Caldwell (1962a) believes that all references to green turtles off California and northward along the coast should be considered as indicating carrinegra and he gives a detailed account of this subspecies. However, the problem of distinguishing this subspecies from black agassizii along the Mexican and Guatemalan coasts still remains to be solved. If this cannot be done, the proper name for the black turtle will be Chelonia mydas agassizii (Hirth and Carr, 1970).

According to local inhabitants, two fairly well marked stocks of Chelonia (or a variably coloured single population) occur in the Galápagos area (Carr, 1964). The turtle situation here warrants immediate study.

Carr (1964) has noted some carrinegra characteristics in some turtles in the Hawaiian Archipelago. The concurrent distribution of carrinegra-like and mydas-like forms in the Central Pacific may indicate a tendency toward polymorphism within a single population (Hirth and Carr, 1970).

Chelonia mydas japonica (Thunberg) is the name given to the Western Pacific green turtle (see Carr, 1942 for discussion). The type locality is Japan. Wermuth and Mertens (1961) give the range as Pacific and Indian Oceans. Okada (1938) lists japonica from Honsyu, Sikoku, Kyusyu, Bonin Islands, Okinawa and Taiwan. The Hawaiian Islands probably represent the easternmost outpost of this subspecies (Oliver and Shaw, 1953). Honegger (1967) and Gaymer (1968), but not Hirth and Carr (1970), use this trinomial for the Seychelles population. Other workers in the Indo-Pacific region, notably Deraniyagala (1939), Suvatti (1950), Harrisson (1950-1969), and Hendrickson (1958) have also deferred from identifying the subspecies.

Taylor (1920) describes Chelonia mydas japonica from the Philippines as follows: above rusty reddish brown, each shield streaked with amber; head shields distinctly reddish, each edged with black; shields on sides of head dark, with yellow along sutures; shields on legs with black centres; plastron yellow. Taylor (1970) briefly describes adult japonica from Thailand as greenish to greyish brown, some individuals with dark rays; and the plastron yellow. He goes on to say that the young are also olive to dark brown with some yellow markings on the limbs; venter yellowish; and dark areas on flippers.

There are probably several races scattered throughout the Pacific Ocean and the Indian Ocean and as already stated, the situation warrants a careful systematic study. The books by Deraniyagala (1953), Kuroda et al. (1958), and Anon (no date) include colour illustrations of green turtles from the Indo-Pacific region. A coloured picture of the venter of a green turtle from Indefatigable Island, Galápagos, appears in the article by Johnson and Johnson (1959).

According to Schmidt (1945), because of historical zoogeography, one would expect the marine turtle populations on the Pacific coast of the Americas to be more closely related to those on the Atlantic and Caribbean coasts than to those in the western Pacific. On the other hand, evidence is accumulating (see colour descriptions in preceding paragraphs and below) which suggests just the opposite.

The following accounts of green turtles in the South Pacific (Hirth, MS) are given as a start toward a descriptive classification of all turtles in the Pacific region (although it should be noted that there may be significant colour variations among individuals of the same population and certainly between different sizes). In French Polynesia, a juvenile green turtle with a carapace length of 30.5 cm has a carapace predominantly copper-brown with grey-black rays; the top of the head is black with well-defined sutures and the sides of the head are blackish-brown; the flippers are black above and white below but with the distal half below mottled yellow-black-brown. The throat and plastron are white.

A sub-adult female, carapace length of 68.5 cm, from French Polynesia, has a carapace streaked with copper, yellow, black and brown: the top of the head has a ground colour of black, but most scales have distinct copper spots; the sides of the head are blackish; the dorsum of front flippers are black but with distal one-third edged with copper: the dorsum of hind flippers are predominantly black; venter of all flippers are yellowish with black on distal third; yellowish-white plastron.

Examination of ten adults (eight males; two females) from Scilly, French Polynesia showed no significant colour differences between the sexes. Nine had marked indentations above the hind flippers. All had post-ocular counts of 4/4. A typical turtle with a carapace length of 100 cm has a greenish brown carapace mottled with white, yellow, olive and black; the top of the head is similar to the carapace in colouration; the throat and plastron are white.

A sub-adult green turtle (carapace length 45 cm) from Western Samoa has a brown-green carapace streaked with black; top of head is brown and sides of head black; four flippers above are black with some brown interspersed and below are variegated yellow-black-brown; the plastron is white.

An adult female (carapace length 96.5 cm) from Western Samoa has a dark brown carapace abundantly covered with light green, light brown and yellow spots and blotches; top of head is spotted brown and green; sides of head basically yellow with large black spots in middle of each scale; top of flippers spotted black-brown-green while flippers underneath are yellowish-white with few black spots in middle of each flipper; chin and plastron are yellowish.

An adult female (carapace length 101 cm) from Tonga has a light green carapace heavily mottled with black, dark brown and light brown; top of head is basically greenish-black with blotches of yellow and light brown; sides of the head are basically yellow but with black spots in scales; flippers above are dark copper-brown with black spots and below are whitish-yellow with a few black centred scales: the plastron is yellowish.

Sub-adult turtles (carapace lengths 58.4 and 60 cm) from the Fiji Islands and New Caledonia are very similar in that the carapace is basically brownish-green with distinct copper, yellow and green streaks; top of head is black with large copper spots and sides of head are blackish, fading into white near the lower jaw; flippers above are blackish with copper on forward edge and tips; venter of flippers are white-yellow with some black scales on trailing edge; throat and plastron are whitish-yellow.

The green turtle is an occasional visitor in New Zealand and adults have been described by McCann (1966b) as being olive or brown, the shields with more or less distinct brown rays; and, yellow beneath.

Basically, the carapace of a mature female from the Gulf of Aden and the Seychelles Islands (Hirth and Carr, 1970) is mottled with yellow, brown, black and green. The top of the head is spread with black, green and brown spots, and there are well-marked yellowish seams between the scales. Adult males are similar to females with the exception that males have less yellow and brown mottling on the carapace and top of the head. Whether these pigmentation differences between the sexes are consistent throughout this population is unknown. Deraniyagala (1939) noted some colour differences between the sexes around Ceylon. In general, the pigmentation of the South Yemeni green turtle population is consistent with Deraniyagala's (1939) descriptions of Ceylonese turtles of the same sizes. He describes eight pigmentation phases of the green turtle in which the carapace passes from dark greenish-bronze in the hatchling to a brownish-red phase, then a variegated phase, and ultimately to the olive tint with black and brown streaks characteristic of adults. Boulenger (1890) describes young green turtles from Indian Ocean area as "dark brown or olive above, the limbs margined with yellow; yellow beneath, with a large dark brown spot on the hand and foot. Carapace of adult olive or brown, spotted or marbled with yellowish".

Hoofien and Yaron (1964) describe the carapaces of two adult turtles from the Dahlac Archipelago as uniform ochraceous brown. They also mention the lack of distinct marginal indentations above the hind limbs.

1.24 Common names

Some common names of the green turtle in various areas of the world are given in Table 1. The name "green turtle" is derived from the colour of its fat.

The Raroians (Danielsson, 1956) have names for the various stages in the ontogeny of sea turtles: egg (tōuo vaki), hatchling (karēa), three classes of juveniles (torēarēa, kōpue, mākui), adult (tīfai).

Some Tonga fishermen also have names for the colour phases and various sizes and sex.

1.3 Morphology

1.31 Anatomy

An annotated bibliography of some aspects of the morphology of marine turtles is found in Ingle and Smith (1949). More recently, Bellairs (1970) has written about the general anatomy and physiology of the green turtle. An early account of the anatomy of *Chelonia* was given by Hoffmann (1890). Among the classical works on anatomy are those of Pilliet and Bignon (1885) on the lacrimal gland; Kesteven (1911) on cranial

TABLE I

Common names of the green turtle. The geographical area or language is followed by the vernacular.

Western Hemisphere

North America	green turtle, green sea turtle, edible turtle
Danish West Indies, Trinidad, Tobago	green turtle, edible turtle, greenback
Caribbean Spanish	tortuga, tortuga blanca, tortuga verde
Mexico	la parlama, caguama, caguama comun, caguma negra, tortuga prieta, caguama prieta, mestiza, tortuga negra, sacacillo
Guyana	bettia
Surinam	krape
Tupi in Brazil	suruanã
Hawaiian and Tahitian	honu
Western Samoa	laumei
Tonga Islands	fonu tu'a'uli, fonu tu'akula, fonu tu'apolata, tuai fonu
Fiji Islands	vonu damu, vonu loa, mako loa, ika damu

Eastern Hemisphere

English	green turtle, edible turtle
German	Suppenschildkröte
French	tortue franche, tortue de mer, tortue verte
Portuguese	tartaruga, tartaruga-do-mar, tartaruga verde
Ghana	anjwa, apuhulu, apuhuru, hala
Swahili	kassa
Mozambique	itataruca, nruvi, asa, pateri, casa, icaha
Bajuni of Lamu	taza
Southern Yemen	bissa, bissat al bahr, humsa
Creole on Aldabra Atoll	tortie de mer
Maldive Islands	vela
Sinhalese	gal käsbäva, mas käsbäva, vali käsbäva
Tamil	perr āmai, pāl āmai
Malay on Cocos Islands	penyu
Malaysia	puin, sisek, penyu, penyu agar, penyu pulau
Borneo	pinu
Philippine Islands	pudno, turtuga
Chinese	lu tzu-hsi
Japanese	ao umigame

morphology; Nick (1913) on the development of the skull; Ruckes (1929a, b) on osteology; Deraniyagala (1939) on general ontogeny and scalation; Villiers (1958) on general anatomy; and Parsons (1959) on the nasal cavities. A study of respiratory muscles in mydas has been made by Shah (1962). The total lack of the lung muscle, muscularis striatum pulmonale, is notable. Mlynarski (1961) has described the structure of scutes and Brongersma (1968b) described some variations in vertebral scutes of Surinam turtles.

Parsons (1958) examined the choanal papillae of green turtles but was unable to give it a function. Later, Smith (1961) proposed that the choanal rakers in adult green turtles are correlated with its herbivorous diet.

1.32 Cytomorphology

According to Makino (1952) the female green turtle has one less chromosome than the male. Working with Chelonia mydas japonica from the Bonin Islands, he found, through histological examination, that the diploid number was 56 and 55 in the males and females respectively.

Characteristics of the haemoglobin of C. mydas have been studied by Dozy et al. (1964). Stephenson (1966) relates how the cells of mydas have been used in cell culture studies.

1.33 Protein specificity

The serum protein concentration in Chelonia m. mydas is 1.8% (Frair, 1964). In most turtles it is between 2 and 6%. Serological studies suggest a close relationship among the five genera of sea turtles (Frair, 1969).

1.4 Measuring and tagging turtles

The standard measurements of sea turtles (all of which are straight-line distances) are length and width of carapace, length of plastron and width of head (see Fig. 2). The lengths of plastron and carapace are anteriormost to posteriormost extensions of each. The width of the carapace is the distance between its lateral margins at the widest point. The head measurement is taken at the greatest bony width.

The most common method of tagging marine turtles employs the use of a stainless steel tag clamped onto the trailing edge of a front flipper (see Fig. 3). The tags are numbered on one face and on the other side are inscribed instructions for the finder in various languages. Adult females are usually the only ones tagged because they can be easily caught on the nesting beach. One of the problems in sea turtle biology is to invent a tag that can be placed on or in a hatchling and which will identify it some years later. Attempts to mark or tag hatchlings by branding, tattooing, and use of magnetic tags have not been successful (Carr, 1967b). Notching marginal scutes is the most common method used today by turtle biologists, but the long-term success of this method has yet to be established. Identifying individuals through immunological reactions has been suggested by Hendrickson (1969). Hughes (1970) in experiments with loggerhead (Caretta caretta) hatchlings is implanting a piece of stainless steel wire under selected carapace scales in hopes of identifying individuals later recaptured by x-raying them (see also Anon, 1969k). Pough (1970) has recently suggested a method of marking hatchlings using a plastic plug.

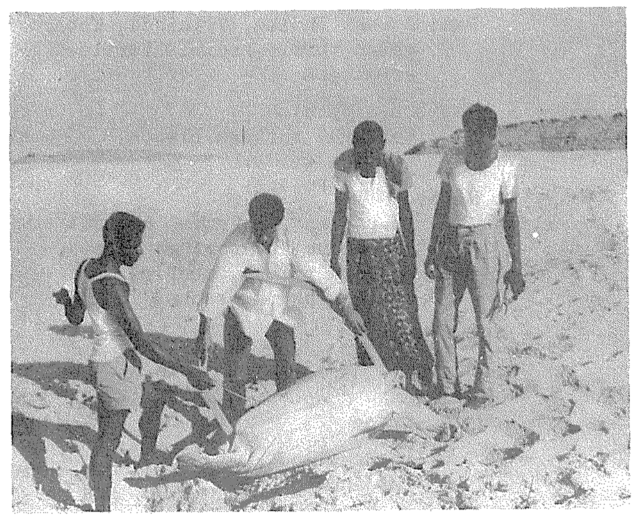

Fig. 2 Measuring the plastron length of a South Yemeni green turtle. The use of "giant" calipers gives straight-line measurements. The man on the right holds a pair of tagging pliars

Fig. 3 A tagged Western Samoan green turtle. The stainless steel tags, numbered and inscribed in various languages, have been adopted by marine turtle biologists throughout the world

2 DISTRIBUTION

2.1 Total area

Green turtles are found throughout the tropical seas and as stragglers in a far more extensive area. The major breeding and feeding areas, and hence the majority of green turtles, are found between the northern and southern 20°C isotherms (i.e., average temperature of surface water in coldest month is above 20°C).

On the American side of the Atlantic Ocean, green turtles have been captured or sighted as far north as New England (Lamson, 1935; Pope, 1939; Dexter, 1947; Bleakney, 1965). Carr (1952) says that individuals have been reported seen in Newfoundland waters but no specimens have been taken. The southern locality record of the green turtle in the western Atlantic is Mar del Plata and Necochea, Argentina (Barran and Freiberg, 1951; Freiberg, 1967).

On the other side of the Atlantic, green turtles have been recorded from the English Channel (Hellmich, 1962) to South Africa (Loveridge and Williams, 1957; Rose, 1962; Hughes, 1970).

The northernmost records for green turtles in the Pacific are Washington State and British Columbia (Carl, 1955; Logier and Toner, 1961; Slater, 1963), Bonin Islands (Stejneger, 1907), Japan (Wang and Wang, 1956), and Korea (Shannon, 1956). They have been reported as far south as the Kermadec Islands (Oliver, 1910), New Zealand (McCann, 1966a, b) and Chiloe, Chile (Donoso-Barros, 1966).

Brongersma (1961) believes that the dead green turtles that have been found on the Dutch coast were released from passing ships. In 1952 a live juvenile Chelonia (carapace length 36 cm) was stranded near Petten on the coast of the Netherlands, but it is unknown whether this too was released by man.

Few Chelonia have been sighted off the western coasts of South America and Africa south of the Tropic of Capricorn, and none have been seen south of 40°S latitude on the eastern coast of South America. The lack of records in these southern latitudes may be due to the fact that the dominant surface currents in these regions (Peru or Humboldt Current, Falkland Current, Benguela Current) are cold currents.

This synopsis does not include references to strictly random sightings of green turtles. However, such records should be pooled and analysed in order to determine if cryptic patterns of movement and distribution do exist. For example, the sightings of turtles in the shipping lanes of the North Atlantic warrant plotting and study.

Man's activities and depredations on green turtle nesting beaches (taking adults and eggs for food; construction of dwellings, roads) have eliminated some good nesting sites and hence the distribution of green turtles has been reduced (see section 5).

2.2 Differential distribution

2.21 Hatchlings, juveniles and sub-adults

It is postulated that the hatchlings leaving Ascension Island drift downstream (i.e., toward Brazil) with the South Equatorial Current (see section 3.53).

There is a dearth of information on the bionomics of hatchlings and juveniles. In fact, the first year of life of all marine turtles has been popularly labelled "the lost year" by marine turtle biologists (see Brongersma, 1970).

Developmental migrations of juveniles and sub-adults are discussed in section 3.51.

2.22 Adults

The distribution of adults is determined to a large extent by the location of their nesting beaches and their feeding grounds. James J. Parsons (1962) has written an elegant book in which he documents and describes many of the nesting sites around the world. The important still extant sites, as well as recently discovered nesting beaches, are summarized in the following sections.

The well-known nesting areas are cited in Table II and Figs. 4 and 5. All the major nesting beaches are within 26°N or S of the equator. The majority of the beaches are on islands. Heron Island and Europa Island are the two most southerly major breeding sites of the green turtle; beaches on the coast of West Pakistan, Baja California and in the Hawaiian Islands are the most northerly rookeries.

Some lesser-known green turtle rookeries are cited in Table III. Most of these are also on islands.

In addition to the rookeries cited in Tables II and III, nesting has been recorded in various other places in the tropics. These nesting locales are given below. In some of these places the season or density of nesting is unknown and in other cases the beaches are probably no longer used by green turtles.

Distribution in the Pacific Ocean and adjacent seas.

Green turtles have been sighted or caught off the Pacific shore of Panama (Evans, 1947), Peru (Murphy, 1925) and Chile (Yañez, 1951) but nesting beaches on these shores are unknown.

Nesting on Islas de Revillagigedo and Baja

TABLE II

Some major green turtle nesting sites

Locality	Nesting Season	Peak of Nesting	Authority
WESTERN HEMISPHERE			
Michoacan Coast, Mexico	-	May-September	Peters, 1954, 1956-57 Duellman, 1961 Montoya, 1969
Tortuguero, Costa Rica	June-Nov.	late July-early Sept.	Carr and Ogren, 1960
Shell Beach, Guyana	March-August	probably June-July	Pritchard, 1969
Bigi Santi, Surinam	Feb.-August	April-May	Pritchard, 1969 Schulz, 1969
Isla Aves	March-Dec.	probably July	Parsons, 1962 Lazell, 1967 Morice, 1958 Hirth (MS)
EASTERN HEMISPHERE			
Ascension Island	Dec.-June	Feb.-April	Carr and Hirth, 1962
Southern Yemen	probably year around	one peak in November	Hirth and Carr, 1970
Hawke's Bay, West Pakistan	year around	late June-early Nov.	Hatt, 1957 Minton, 1966
Aldabra Atoll	year around	February-May	Hornell, 1927
Europa Island	year around	-	G.R. Hughes (MS) J.Y. Cousteau (film) Parsons, 1962
Ko Khram, Thailand	year around	May-July	Penyapol, 1958
Malaysia	year around	July-August	Harrisson, 1951, 1952, 1965a Hendrickson, 1958 de Silva, 1969a
Indonesia	probably year around	-	Somadikarta, 1968
Philippine "Turtle Islands"	year around	August	Domantay 1952-53, 1968
Heron Island, Australia (and other Capricorn Group Islands)	Oct.-March	January-February	Moorhouse, 1933 Bustard, 1967a, (MS)
Bountiful Is., Australia (and other islands in Gulf of Carpentaria)	June-Feb.	?	Bustard (MS) Parsons, 1962

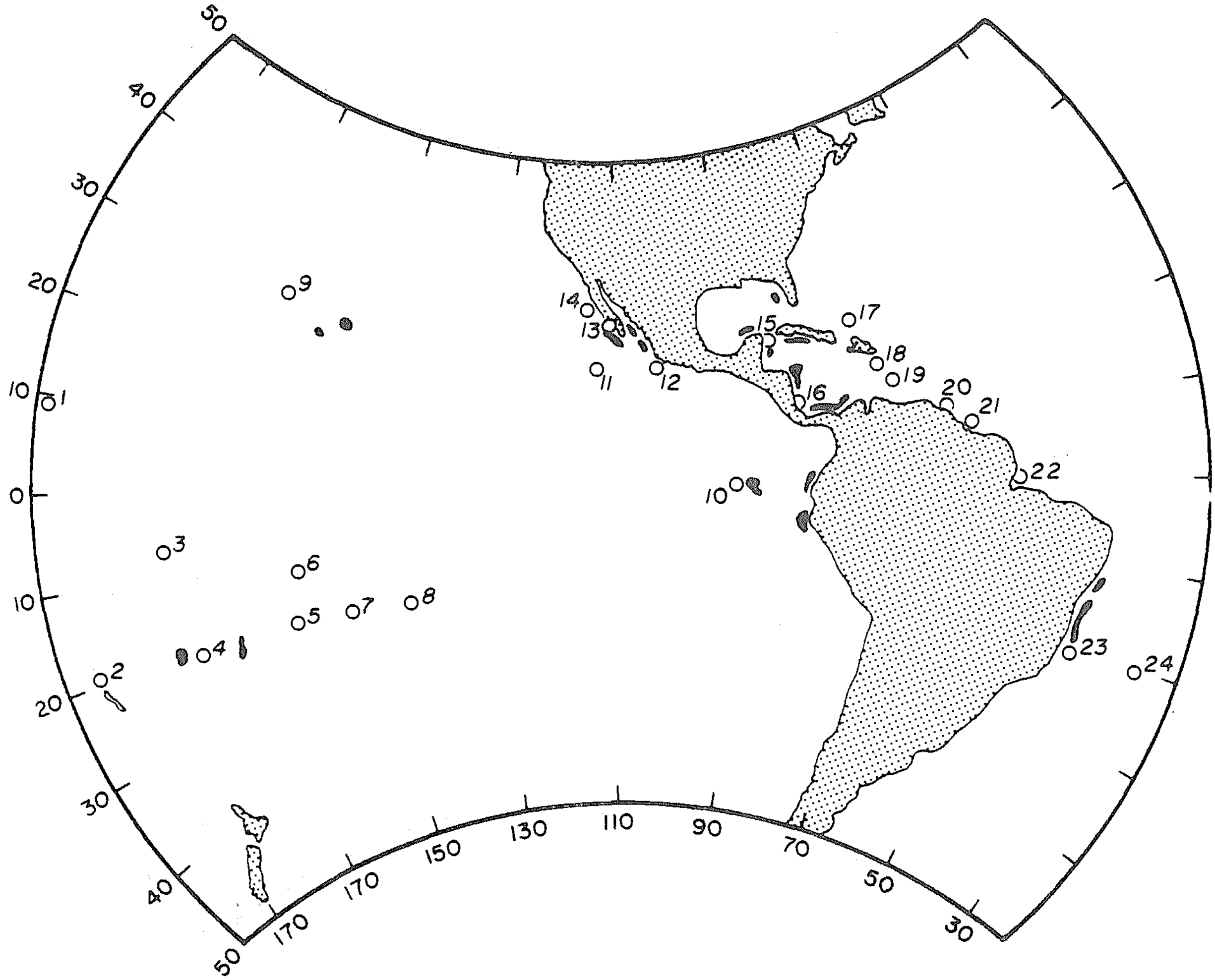

Fig. 4 Some of the important green turtle nesting beaches (numbered circles) and feeding grounds (shaded areas) in the western hemisphere. Modified from Parsons (1962) and Carr (1965). 1 = Ujelang, 2 = D'Entrecasteaux, 3 = Funafutio, 4 = Vatoa, 5 = Palmerston, 6 = Rakahanga, 7 = Scilly, 8 = Raroia, 9 = French Frigate Shoal, 10 = Galápagos, 11 = Clarion, 12 = Michoacan coast, 13 = Bahia Magdelena, 14 = Bahia San Bartolome, 15 = Quintana Roo, 16 = Tortuguero, 17 = Little Inagua, 18 = Mona, 19 = Aves, 20 = Guyana beaches, 21 = Surinam beaches, 22 = Marajo, 23 = Rio Doce, 24 = Trindade

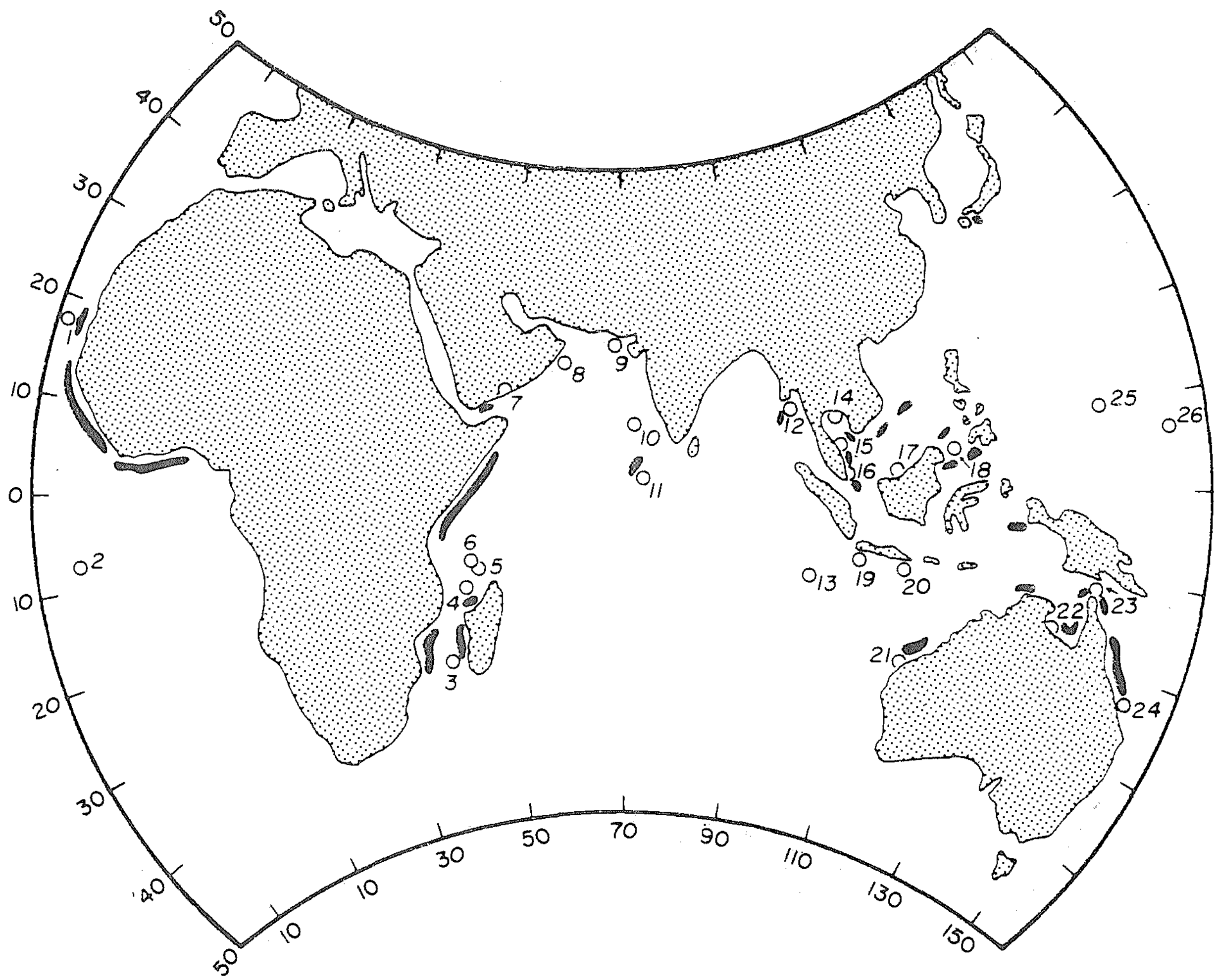

Fig. 5 Some of the important green turtle nesting beaches (numbered circles) and feeding grounds (shaded areas) in the eastern hemisphere. Modified from Parsons (1962) and Carr (1965). 1 = Cape Verde Islands, 2 = Ascension, 3 = Europa, 4 = Comores, 5 = Astove, 6 = Aldabra, 7 = Southern Yemen beaches, 8 = Masira, 9 = Hawke's Bay, 10 = Laccadives, 11 = Maldives, 12 = Diamond, 13 = Cocos (Keeling) Is., 14 = Gulf of Thailand beaches, 15 = Songkhla, 16 = West Malaysia Islands, 17 = Sarawak turtle islands, 18 = Philippine turtle islands, 19 = Schildpad, 20 = Baroeng, 21 = Flying Foam Is., 22 = Gulf of Carpentaria Islands, 23 = Torres Strait Islands, 24 = Heron Island, 25 = Central Caroline Islands, 26 = Oroluk

TABLE III

Season of nesting at some lesser-known and minor green turtle rookeries

Locality	Nesting (by months) J	F	M	A	M	J	J	A	S	O	N	D	Authority
						Pacific Ocean and adjacent seas							
Chiapas, Mexico							X	X	X	X	X	X	Alvarez del Toro, 1960
Galápagos Is.	X	X	X									X	P. Pritchard (MS)
Rose Atoll								X	X				Sachet, 1954
French Polynesia										X	X	X	Chabouis, L. and F., 1954 Hirth (MS)
Tonga Islands	X	X									X	X	Hirth (MS)
New Caledonia	X											X	Hirth (MS)
Bikar Atoll, Marshall Is.								X					Fosberg, 1969
Jemo Island, Marshall Is.												X	Fosberg, 1969
Houtman Abrolhos, Australia	X											X	Storr, 1960
						Atlantic Ocean and adjacent seas							
Yucatan Peninsula					X	X	X	X					R. Marquez, pers. comm.
West Indies				X	X	X	X	X					Underwood, 1951
Coast of West Africa	X								X	X	X	X	Gadow, 1909
Senegal							X	X	X				Cadenat, 1949 Villiers, 1958
Fernando Poo, Gulf of Guinea	X	X									X	X	Eisentraut, 1964
						Indian Ocean							
Maziwi Is., Tanzania		X	X	X	X	X	X	X					Anon, 1969b
Dahlac Archipelago			X										Anon, 1969a; Urban, 1970
Astove and Cosmoledo in Seychelles Is.		X	X	X									Hirth and Carr, 1970
Jurayd Is., Persian Gulf						X	X						E. Hoag, pers. comm.
Masira Is.						X							Parsons, 1962

California is mentioned by Beebe (1937), Brattstrom (1955) and Parsons (1962). These areas should be reconnoitred again, with special emphasis on assessing nesting aggregations.

In former years green turtles were readily caught in waters off the Hawaiian Islands especially near Oahu, Molokai and Maui. Today the majority of nesting is on French Frigate Shoal in the Hawaiian Leewards. Especially large concentrations of basking turtles have been seen on Pearl and Hermes Reefs and somewhat smaller concentrations on Lisianski Atoll and Layson Atoll, all in the Hawaiian Leewards. Hendrickson (1969) and Northshield (1969) report green turtles are still found in the Leewards, but are scarcer than they used to be. Now that the Leeward Islands are under the guardianship of the U.S. Bureau of Sport Fisheries and Wildlife, the turtle population may stabilize or even increase. In any case, whatever is left of the original population, the Hawaiian Leewards remain the biggest green turtle rookery in the United States.

Parsons (1962) and Wiens (1962) have documented the occurrence of green turtles in Melanesia, Micronesia and Polynesia. In earlier days Chelonia nested in fairly large numbers on Ulithi, Ifaluk, Gaferut, Elato, Olimarao, Fanning Atoll, Christmas Atoll, D'Entrecasteaux Reefs (July through October), American Samoa (August and September), Oroluk Atoll, Raroia (June through September) and Vatoa. The density of nesting on Palmerston Atoll now is unknown, although Carr (1965) lists it as a major nesting beach. There may still be a large nesting colony on Palmerston and the situation warrants immediate attention. Preliminary attempts at assessing turtle stocks in the South Pacific have been made by Anon (1969f) and Bustard (1969a).

Green turtles nest occasionally on the sandy beaches of Arno Atoll in the Marshall Islands but they are scarce and of no commercial importance (Hiatt, 1951). They are now rarely seen around Kapingamarangi Atoll in the Caroline Islands where they once were an important source of food (Niering, 1963). They are reported to nest in the Helen's Reef area about 480 km southwest of Palau and on a small island north of Palau and just off the island of Kayangel, all in the Caroline Islands (Wilson, 1969). Carr (1965) cites nesting on Ujelang in the Central Carolines and on Funafutio and Rakahanga in the South Pacific. Neill (1958) provides a few references to early accounts of green turtles in the western Pacific and Indian Oceans. Dr. John Hendrickson (University of Arizona) is currently studying the marine turtle populations in Micronesia.

As far as is known, the extent of nesting in the Ogasawara Islands (= Bonin Islands) has not been elaborated on since Okada's (1931) account which included statements that mating takes place from March to May and eggs are laid from May through August. Makino (1952) also referred to nesting in the Bonin Islands; and in 1968 Sampson mentioned hunting "sea turtles" close to shore. If still extant, this would constitute one of the most northerly breeding sites of Chelonia.

On the western perimeter of the Pacific Ocean, green turtles have been reported from Amami-oshima in the Loo Choo Islands (=Ryukyu) (Koba, 1959) and from Taiwan (Gee, 1929-30). Pope (1935) cites references pertaining to green turtles laying eggs on islands near Hong Kong in July and August. However, nesting here now seems very doubtful.

The density of nesting today on Pulau Berhala off Sumatra is unknown, but Mohr (1927) noted oviposition every month with a peak from November to January. De Rooij (1915) listed mydas as occurring on the following islands of the Indo-Australian Archipelago: Sumatra, Biliton, Borneo, Java, Madura, Flores, Celebes, Ambon, Banda Obi, Aru and New Guinea. Pangumbahan, a nesting site on the south coast of Java, where a large number of eggs are harvested, is described by Reksowardojo (1961). Somadikarta (1962) lists some nesting beaches in Indonesia which are rented out for their eggs. Some, no doubt, are green turtle rookeries. Parsons (1962) describes nesting near Barceng in Java. A thorough taxonomic and ecologic study should be made of the green turtles in Indonesia. Especially since the Archipelago occupies a unique position between the Indian Ocean and South China Sea.

In addition to the large Sarawak rookeries in Malaysia (see Table II) green turtles also nest on small coastal islands in West Malaysia. The most important of which are the Perhentian and Redang Islands off the coast of Kelantan and Trengganu (Hendrickson, 1961).

Besides the well-known Philippine "Turtle Islands", (see Table II) other islands in the Sulu Sea where some nesting occurs include Cavili, Arena, Lumbucan, Bancoran and San Miguel (Martin, 1952-53).

Cockcroft (1968) stated that green turtles are common in warm waters off Papua, and Hurley (1924) briefly described nesting on a small island in the Torres Strait.

Copulating pairs have been seen in September and October off the beaches in Northern Territory, Australia, and reliable sources indicate large nesting aggregations on islands in the Gulf of Carpentaria (Cogger and Lindner, 1969; Bustard, MS). Evidently there is large-scale nesting on the western coast of Australia if the following quote is reliable: "All along the northern beaches of the mainland coast (of western Australia) and selected off-shore islands, thousands of female green turtles leave their natural environment—the sea, to make a difficult and exhausting journey onto the land to lay their eggs" (Anon, 1969c). Another article reports nesting near Onslow in Western Australia (Anon, 1970e). Mating is reported off the Great Barrier Reef in October and November (Roughley, 1951).

Distribution in Atlantic Ocean and adjacent seas

Green turtles nest on Papaya Beach, Turtle Beach, Leguan Beach, Tiger Island Beach, Suddie Beach, Zeelandia Beach, Mahaica-Mahaicong Beach and Shell Beach (March through August) in Guyana; on Silebache Beach in French Guiana; and on Bigi Santi Beach and on the strand near the mouth of the Marowijne River in Surinam (Pritchard, 1969). Frair and Prol (1970) saw many green turtles nesting in May in Surinam.

In addition to the references given in Table II some pertinent accounts of the rookery on Aves Island can be found in articles by Zuloaga (1955) and Phelps and Phelps (1957). Aves is the only above-water part of the so-called "Aves Swell". The island is almost surrounded by a reef and the maximum elevation above sea level is 3.5 m. The island is also a well-known tern rookery. The fact that the island is sinking raises the question of what returning, oviferous turtles will do when there is not enough beach left for nesting. Morice (1958) states that it is possible to capture from 150 to 200 females in a few nights during June and July on Aves Island.

The Ascension rookery has been briefly mentioned by Packer (1968) besides the authorities cited in Table II. In addition to its remote location, this colony is different from some of the other major rookeries in that the incubating eggs are rarely taken by any predators but entrance to some of the beaches is made hazardous by the combination of heavy seas and rocky shoreline.

Some of the much lesser-known rookeries in the Caribbean and western Atlantic are listed in Parsons (1962). These include Isla Mujeres and other coral islands off the coast of the Yucatan Peninsula (see also Fosberg, 1962; Mexico, 1966) Mona Island; Marajó Island; beaches near Rio Doce and Cabo Frio on the Brazilian coast and Trindade. Barth (1962) has described the nesting beaches on Trindade, but there is a dearth of information about the breeding colony there. Green turtles have also been seen off the shore of Queimada Grande, about 70 km southwest of Santos, Brazil (Mertens, 1955).

Parsons (1962) cites nesting in the Cape Verde Islands. Brongersma (1968a) quotes the work of Sarmento (1948) which mentions the presence of juvenile green turtles around the Madeira Islands and Brongersma himself describes a juvenile (carapace length 30.4 cm) captured off Madeira.

The northwest bulge of Africa is one of the least known areas as far as marine turtles are concerned. C. mydas appears in a glossary prepared by Osorio de Castro (1954) and is simply listed in the fisheries of coastal Portugal, Azores, Madeira, Morocco and Senegal. Pasteur and Bons (1960) state that it is probable that at least stray green turtles can be found off Morocco.

Distribution in the Indian Ocean and Mediterranean Sea

Green turtles are reported as very common in Mozambique waters and need better protection on the nesting beaches (Anon, 1970i). Today there is only scattered nesting on the coast of Kenya (C. Ray, pers. comm.). Oviposition has been observed on the Somali coast (Cozzolino, 1938; Travis, 1967).

The photograph in the Aramco Handbook (Arabian American Oil Company, 1968) with the legend "Giant Sea Turtles Breed on Islands in the Arabian Gulf" is probably a green turtle. There are also scattered reports of green turtles off Iran in the Persian Gulf.

Green turtles were reported as very common in the Maldives some forty years ago (Deraniyagala, 1956). Nesting on Comores Islands, Diamond Island and Cocos Island is documented by Parsons (1962). The current status of these islands as nesting sites is unknown.

Shockley (1949) along with Hatt (1957) and Minton (1966) describes nesting in West Pakistan (see Table II).

Several people (Bodenheimer, 1935; Haas, 1951; Howells, 1956) have reported the presence of Chelonia on the Israeli coast. The area between El Arish and Hedera is sometimes named as a nesting site; however, it is highly unlikely that turtles nest there now. A couple of Chelonia were caught near Malta some forty years ago (Despott, 1931). C. mydas is reported as uncommon in the Adriatic Sea (Redl, 1963). The green turtle along with loggerhead and hawksbill turtles has been observed off southern France (Knoepffler, 1961).

The only known breeding colony of any size in the Mediterranean is the rookery on the southern coast of Turkey near Marsin and Yamortalik (Anon, 1967a). According to Mr. I. Sela of Israel, the colony is rapidly diminishing due to overexploitation. The rookery is now being investigated by Dr. R.W. Hathaway (University of Utah).

In some places in the Mediterranean the reports of Chelonia are questionable because some reporters have had difficulty in distinguishing the green turtle from the loggerhead turtle.

Green turtles are very rare in the Black Sea. One was caught near Sozopol in Bulgaria about 70 years ago (Valkanov, 1949; Fuhn and Vancea, 1961).

Location of feeding pastures

Some of the principal feeding pastures are: upper west coast of Florida; northwestern coast of Yucatan peninsula; south coast of Cuba; Mosquito coast of Nicaragua; Caribbean coast of Panama; scattered areas along Caribbean coast of Colombia; scattered areas off Brazilian coast; west African coast from Mauritania to Nigeria (see Villiers, 1958, 1962 for descriptive accounts); Mozambique Channel; Bajun Islands and neighbouring coast of Somalia; Khor Umaira in the Gulf of Aden; Maldive and Laccadive Archipelagoes; around Ceylon and Krusadai Island (see Deraniyagala, 1939, and Kuriyan, 1950); scattered areas in the South China Sea and in the Gulf of Thailand; northern sector of the Great Barrier Reef; Torres Strait; Gulf of Carpentaria; Flying Foam Islands; Hawaiian Islands; around some of the Fiji Islands and Tonga Islands; Pacific coast of Baja California; Gulf of California; Galápagos Islands, and parts of the coasts of Ecuador and Peru. Figs. 4 and 5 indicate the approximate limits of some of the better known feeding areas. As is to be expected, the most extensive pastures are along continental shelves.

There are several lesser known feeding areas. Green turtles are reported grazing between January and March near Sunday Island in the Kermadec Group (Oliver, 1910). They do not breed in the islands but are reported to go north for mating. Individuals have been seen feeding on the bottom in shallow waters off Northern Territory, Australia (Cogger and Lindner, 1969; Bustard, MS), and _mydas_ is reported as a staple item in the diet of a small number of coastal aboriginals still living a tribal way of life.

In the Fiji Islands green turtles can be seen feeding in the passage between Taveuni and Vanua Levu (Bustard, 1970b). Hirth (MS) has found feeding pastures around Viti Levu in the Fiji Group as well as around Tongatapu in the Tonga Islands.

Very little is known about the population dynamics, productivity or activities of green turtles on the feeding pastures - this in spite of the fact that a turtle probably spends most of its life there.

2.3 <u>Determinants of distribution changes</u>: see sections 2.1, 2.2, 3.16, 3.22 and 3.5

2.4 <u>Hybridization</u>

Nothing is known of hybridization in nature. The author suspects, however, that hybridization would occur if turtles are able to pass through the newly proposed cross-Panama Canal; and, if captive turtles escape from turtle farms.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Green turtles are heterosexual. Adult males have a very long, somewhat prehensile tail reaching as far as or beyond the extended hind flippers. The tail of the adult female rarely extends beyond the margin of the carapace. Males also have longer claws on their front flippers than do females. Some investigators have had difficulty in determining the sex of hatchlings, but Makino (1952) states that the sexes of even embryos can be determined by histological examination. According to him, the embryonic ovary of C.m. japonica is easily distinguishable from the testis by having a thick and elongated cortical layer of primordial germ cells which show active proliferation. The testis is a little shorter in length but much thicker than the ovary of the same age. He goes on to say that the testis is further characterized by the fact that the primordial germ cells develop as solid cords of irregular shape towards the medullary region of the gonads. Further histological studies are now in progress in the laboratories at the University of Utah.

3.12 Maturity

Investigators are not certain at what age green turtles reach maturity. Estimates are four to six years (Hendrickson, 1958), at least six years (Carr, 1967b), at least seven years (Harrisson, 1962d), five to seven years (Ehrenfeld, 1970) and eight to thirteen years (Caldwell, 1962c). The age, or size at which sexual maturity is reached may of course vary between individuals of the same population and also between individuals of different populations. For example, Carr and Carr (1970b) have discussed the variation in maturation size at the Tortuguero rookery. Evidently this population includes two kinds of big turtles: some that grew big after reaching sexual maturity, and some that reached maturity at a large size.

The smallest nesting females recorded on the Tortuguero and Southern Yemen breeding beaches had carapace lengths of 69.3 and 78.7 cm respectively (Carr and Ogren, 1960; Hirth and Carr, 1970). Sizes of nesting females at some of the better known nesting beaches are given in Fig. 6. Corresponding weights can be ascertained from Fig. 7.

3.13 Mating

Copulation usually occurs just off the nesting beaches, usually within one kilometre of shore. It is unknown whether the males accompany the females from feeding pastures to nesting grounds or whether they make a synchronized rendezvous with the females at the rookery. At some of the larger breeding areas (i.e., Tortuguero, Sarawak Islands, Bountiful Island, Aldabra Atoll) one female is usually attended by several males and males show an interest in any female. This suggests that polyandry may be the *modus operandi*, but it may also be a reflection of the fact that females, but never males, are exploited on the nesting grounds. Or it may reflect on the fact that all males remigrate (= periodic movement out from and back to the original area) to the nesting ground every year while most females have a biennial or triennial cycle. However, it seems unlikely that males do remigrate each year because of the bioenergetic requirements of such extended travel. On the other hand, the preponderance of males may not be real at all but merely a reflection of the male's very intense activity during the breeding season. It is also possible that the sex ratio may indeed be in favour of males at the start of the breeding season but that it shifts to an equal sex ratio as the season progresses due to arrival of more females or due to males leaving. It is noteworthy that at Tortuguero, nesting continues after mating activity has ceased and males have virtually vanished from sight.

Of course, the preponderance of adult males off some nesting beaches may also be explained by an unequal sex ratio at hatching or a sexual advantage during ontogeny (see section 4.11).

The question of when the eggs of virgin females are fertilized remains an enigma. It is hypothesized that the young females accompany the older turtles to the nesting ground, mate there and return to home pastures without laying (Carr and Hirth, 1962). Also, according to Carr (1965), "It seems unlikely that any of the eggs of the current season are fertilized as a result of current mating. The encounter probably serves to fertilize eggs for the next nesting season, two or three years ahead". This storage of spermatozoa may account for the infertility of large numbers of eggs (see section 3.16). Mr. Montoya of Mexico reports (pers. comm.) that fertility in C.m. agassizii eggs is higher in the first clutch of the season than in later clutches.

Some aspects of courtship and copulation off the Tortuguero rookery are given by Carr and Giovannoli (1957). They describe how pairing is a strenuous and clumsy operation during which the female is often gnashed and scraped. The enlarged claw on the front flippers of the male aids him in grasping the fore edge of the shell of his mate.

It is plausible that some mating takes place at the feeding grounds or at other areas away from the nesting beaches, although this has yet to be documented.

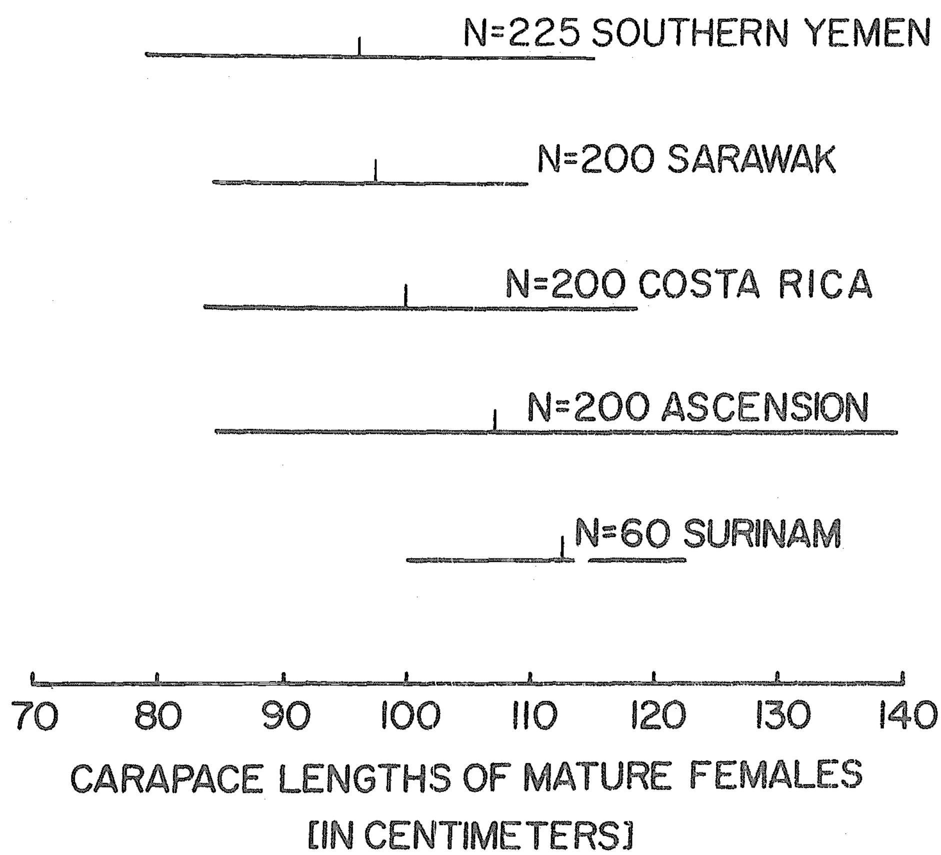

Fig. 6 Sizes of nesting females at some major nesting sites. The length of the horizontal line indicates the range and the vertical line the mean. Data on the Sarawak population are taken from a graph in Hendrickson (1958). Other data are from Carr and Hirth (1962), Pritchard (1969) and Hirth and Carr (1970)

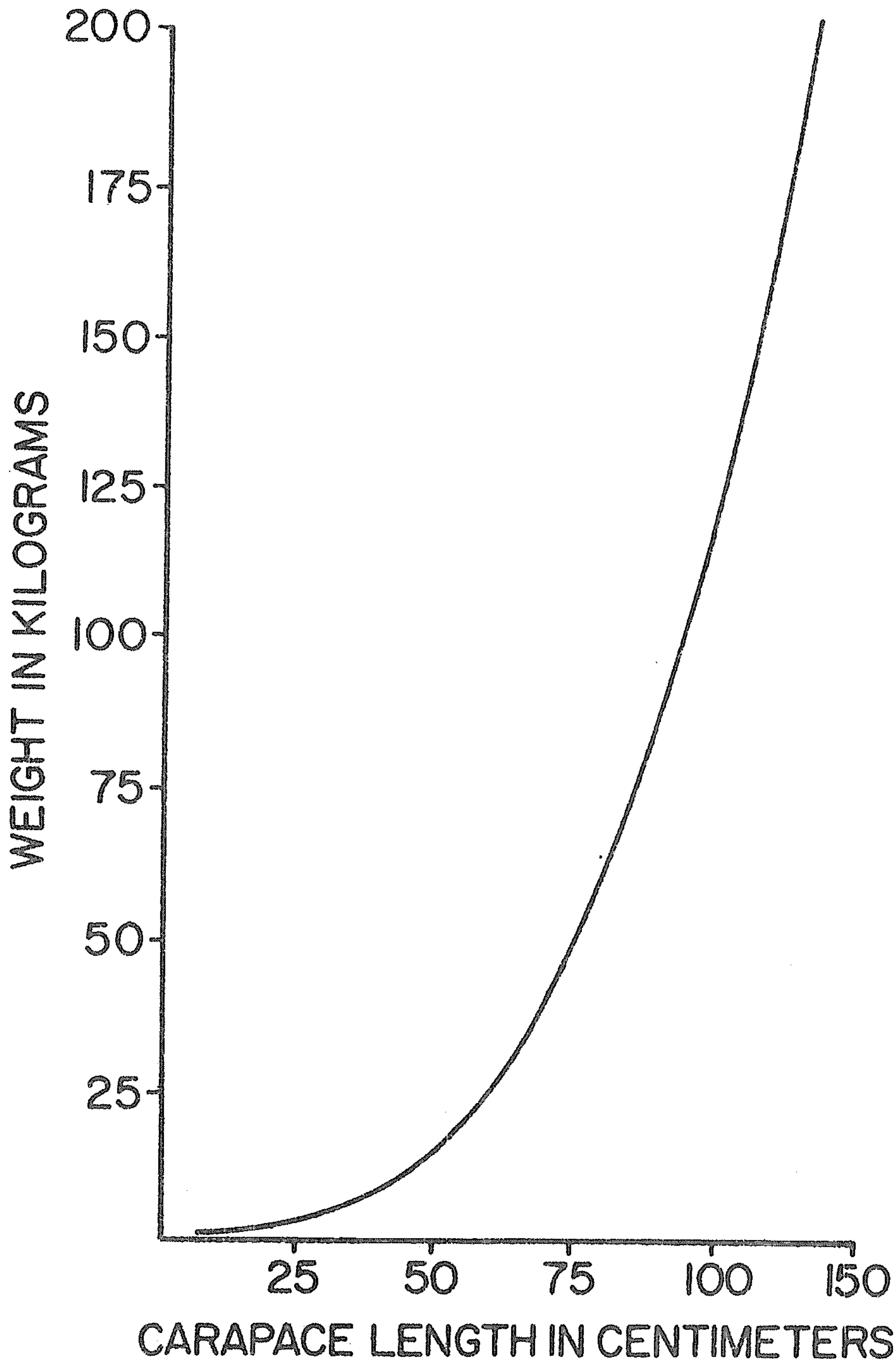

Fig. 7 Model showing weight and carapace length of green turtles (both sexes). Adapted from Hirth and Carr (1970) and based mainly upon turtles caught in the Gulf of Aden feeding pastures

3.14 Fertilization

Fertilization is internal. The question of delayed fertilization is discussed in the preceding section.

3.15 Gonads

See following section.

3.16 Reproductive cycle, nesting behaviour and selection of nesting beach

Man is most familiar with two relatively short phases of the life history of the green turtle - the nocturnal egg-laying behaviour of the adult female, and the subsequent two months of incubation and hatching.

Green turtles nest every four years in eastern Australia (Bustard and Tognetti, 1969), every three years in the South China Sea (Harrisson, 1956b; Hendrickson, 1958) and every two or three years in the Caribbean and South Atlantic, but with the triennial cycle predominant (Carr and Ogren, 1960; Carr, 1965). Recently Carr and Carr (1970a) have accumulated evidence which indicates that a four-year reproductive cycle may also exist in the Costa Rican population. Moreover, they have shown how, although an individual usually maintains a constant cycle, modulation may occur and the change may be either from a three to two year cycle or vice versa. It is postulated that the phase-shift reflects ecological conditions on the feeding grounds. Thus, individuals nesting in any one given year on some beaches around the Atlantic represent four sources: (1) newly matured individuals, (2) returning individuals nesting on a biennial cycle, (3) returning individuals nesting on a triennial cycle, and (4) individuals experiencing a phase-shift in their reproductive cycle. Oviferous turtles may converge on the rookeries from different feeding pastures, some of which may be long distances from the breeding beach.

Most nesting takes place at night, although daytime nesting does occur occasionally on uninhabited Pacific atolls and has been seen in Colombia (Medem, 1962) and Surinam (Pritchard, 1969). The time of year when nesting begins and the duration of the nesting period vary from one region to another (Tables II and III). In some places, such as Malaysia, there is year-round nesting but with specific peak months, while in other places such as Ascension Island, nesting is restricted to a few months of the year. At Tortuguero, a mainland beach where nesting is seasonal, the turtles appear in large numbers rather suddenly, but tend to trickle away at the end of the season.

Most green turtles lay between three and seven times each season at about ten to fifteen day intervals. Hendrickson (1958) stated that about 96% of 5,748 nesting green turtles in the three Sarawak Islands returned to the same island for renesting during the reproductive season even though two of the islands are only about 500 metres apart.

Renestings on the Tortuguero beach are usually within 0.4 to 1.2 km of the preceding nesting emergence (Carr and Ogren, 1960), even

TABLE IV

Basic reproductive data at some major nesting beaches. The range is given in parentheses following the mean.

Locality	No. eggs per nest	Incubation period in days*	Renesting interval in days	Authority
Tortuguero	110 (18-193)	55.6 (48-70)	12.5 (9-16)	Carr and Hirth, 1962
Surinam	142 (87-226)	-	13-14	Pritchard, 1969
Ascension	115.5 (53-181)	59.5 (58-62)	14.5 (10-17)	Carr and Hirth, 1962
Sarawak	104.7 (3-184)	57-70 (depends on season)	10.5 (8-17)	Hendrickson, 1958
Australia	110 (50-200)	68.7 (65-72)	14	Moorhouse, 1933 Bustard, 1967a

* Incubation period is defined as the period between oviposition and emergence of the largest number of hatchlings on the surface

though the beach topography changes from year to year. Apparently, the males roam about just offshore during the mating season.

In order to find out what females do between nestings, a couple of mature individuals at Tortuguero were rigged with helium balloons and kept under visual observation (Carr, 1967b). One individual that was allowed to nest was tracked the next day swimming around off the nesting beach. Another individual that was not permitted to nest struck out in a southeasterly course for about six hours, but the following night returned and nested near the point where she was released. Further studies on this subject using turtles rigged with transmitters are now being conducted at Tortuguero (Carr, pers. comm.)

Table IV compares some basic reproductive data at some of the major nesting beaches. It appears that in addition to being among the biggest green turtles in the world, the females nesting in Surinam have the greatest fecundity. Banks (1937) studied oviposition in the Sarawak turtle islands between 1932 and 1935 and found that the average number of eggs laid by each turtle, based upon thousands of records, varied from 106 to 118. The average number (and range) of eggs per nest at some of the other nesting grounds are as follows: Indonesia, 118 (48-175) (Mohr, 1927); Sabah, 105.6 (72-144) (Harrisson, 1965a) and Southern Yemen, 106 (70-130) (Hirth and Carr, 1970). Harrisson (1962c) describes the monthly laying cycles in Sarawak. Bustard (1967a) found that clutch size increases with age or size of the turtle. On the other hand, Domantay (1952-53) states that younger turtles lay more eggs than older ones.

Carr (1967b) states that at Tortuguero the female lays more than 100 eggs on her mid-season trip ashore and fewer on her first and last trips. On Ascension Island the first and second egg complements of each turtle are usually bigger than the third (Carr and Hirth, 1962). In the Ogasawara Islands, Fukada (1965) reports that each turtle lays between one and five times each season and that each clutch consists of about 70 to 150 eggs. He observed four individuals through four nestings and no significant correlation was found between the sequence of nestings and number of eggs per clutch except that the last nesting had the fewest eggs in each case. Domantay (1952-53; 1968) has observed several old Philippine turtles go through the entire nesting repertoire and then not lay eggs. Evidently some turtles do not retain their reproductive capacity throughout life. Further studies on this subject are needed, especially in view of the practical importance this would have in the management of the species.

Carr (1967b) has lucidly discussed how the number of eggs laid by a green turtle at each oviposition (i.e., about 100) has adaptive value for the species. Some of these advantages include (1) escape from predation by swamping the predators on the beach and the littoral predators during the first few critical hours in the water, (2) metabolic heating of the nest by a mass of eggs, (3) social facilitation in the climb to the surface, and (4) group orientation in the crawl to the sea. Carr also speculates that hatchlings may regroup somewhere after entering the sea and somehow take more advantage from being a group again.

Metabolic heating of the nest has been studied in several places. In Sarawak, Hendrickson (1958) found a progressive temperature rise (from about 28° to 35°C) in nests of developing eggs and postulated that this might be an important factor in influencing the percent hatch. Carr and Hirth (1961) found that the temperature of a nest on Ascension increased from 27.9 to 29.9° over a 61-day incubation period. In Australia, Bustard and Greenham (1968) found that the temperature within a natural nest of eggs is initially about 25-26°C and that there is a rise in temperature to about 31°C during the latter part of incubation due to metabolic heating.

In addition to the incubation data for some major rookeries given in Table IV, additional information is available for lesser known beaches. Domantay (1952-53) and Penyapol (1958) report average incubation periods of 51-53 and 48-50 days in the Philippine Islands and in Thailand, respectively; Fukada (1965) states that it is 63 days in the Ogasawara Islands; and Hirth and Carr (1970) registered 48-49 days in Aden.

The percent hatch (defined as the number of hatchlings, out of the total egg complement, which successfully reach the surface) varies from season to season in different parts of the world (Table V). Pritchard (1967) states that "the fertility of green turtle eggs is low, a 50% hatching being about average". He also states that egg complements which have been dug up and reburied take longer to hatch than otherwise, but the fertility does not appear to be substantially affected.

Balasingham (1967), in an interesting study with leatherback (Dermochelys coriacea) nests, found that he could increase the percentage of hatchlings from transplanted nests if eggs were buried in clutches of about 50. The enigma of why the leatherback usually lays between 85 and 90 eggs per nest thus becomes more puzzling in view of Balasingham's work. Similar studies should be conducted with green turtle clutches.

The nesting behaviour of the green turtle can be divided into eleven stages (Carr and Ogren, 1960):

1) Stranding, testing of stranding site, and emergence from wave wash

TABLE V

The percent hatch of green turtle eggs. All are reburied clutches in egg hatcheries unless otherwise indicated.

Locality	Percent hatch	Authority
Tortuguero, Costa Rica	50	Carr and Hirth, 1962
Ascension Island	54 (natural nests)	Carr and Hirth, 1962
Malaysia	47	Hendrickson, 1958
	30–79	Harrisson, 1961, 1962a
	53–55	Balasingham, 1965
		Anon, 1967b
Sabah	70–90	de Silva, 1969a
Heron Is., Australia	67	Bustard and Greenham, 1968
	55 (natural nests)	Moorhouse, 1933

2) Selecting of course and crawling from surf to nest site

3) Selecting of nest site

4) Clearing of nest premises

5) Excavating of body pit

6) Excavating of nest hole

7) Oviposition

8) Filling, covering and packing of nest hole

9) Filling of body pit and concealing of site of nesting

10) Selecting of course and locomotion back to sea

11) Re-entering of wave wash and traversal of the surf

Some detailed aspects of the nesting repertoire of the Atlantic green turtle are given in Carr and Giovannoli (1957); Carr and Ogren (1960) and Carr and Hirth (1962). Nesting of the Indo-Pacific form is described in varying degrees of detail by Beebe (1937); Hendrickson (1958); Bustard and Greenham (1969); and Hirth and Carr (1970).

"Sand-smelling" or "sand-nuzzling" by the newly stranded female on the beach has been observed by several people in different localities (Carr and Giovannoli, 1957; Carr and Ogren, 1960; Carr and Hirth, 1962; Hirth and Carr, 1970). The exact function of this mannerism is unknown, but it may involve sensory appraisal of the beach. Evidently this trait is lacking in the Pacific forms (Bustard and Greenham, 1969).

The tendency to make "half-moons" (= non-egg laying emergence in which the trail up and down the beach looks like some form of a parabolic curve) and trial holes may be signs of appetitive behaviour, although they may also be merely forms of reproductive unreadiness. Hendrickson (1958) believes that abandoned nests in advanced stages are due to vibrations in the substrate caused by nesting turtles nearby. This certainly would be of adaptive value on crowded beaches by spacing out the nests (see section 4.5).

The females are very shy when ascending the beach. At this time they can be easily scared (i.e., by barking dogs, lights, etc.) back into the sea. Hendrickson (1958) describes the ascent up the beach to the high beach platform in some detail. When the turtle is digging the nest hole and egg hole, she is much less sensitive to alarming stimuli. Once the consummatory act of egg-laying has commenced, virtually nothing will cause the turtle to stop. It is at this stage that large beach predators can easily kill a turtle. The complete nesting repertoire, i.e., from water's edge back to surf, takes about two to three hours.

At some rookeries there appears to be no direct correlation between phase of the moon or stage of tide and nesting, but around some of the Pacific atolls a high tide does aid the turtle in reaching the beach and most nesting is at this time. In other places indigenous people will claim that most nesting takes place at certain phases of the lunar cycle.

Short of imparting a tendency to pack solid, aerate too freely, or to waterlog, the physico-chemical characteristics of good turtle beaches are not very well known. However, one characteristic common to most rookeries is the presence of a beach platform well above flood tide. It is on such a platform that most nesting takes place. Hirth and Carr (1970) found that the texture and composition of the sand on some major nesting beaches vary widely. For example, the sand on the big rookery at Sharma (Southern Yemen) is composed of particles chiefly in the 0.5 to 0.25 mm class - that is, medium grain sand. The beaches at Ascension and Aves Islands are mainly composed of coarse sands and the beach at Tortuguero is made up of fine sand. Other features of the nesting beach sand vary as much as particle size does. Colour, for instance, varies from olive grey at Tortuguero to white on Aldabra; soluble salt content on Sharma is about one third that at Tortuguero; organic content at Sharma is less than half that at Aldabra and Aves Islands. Pritchard (1966) reports that green turtles lay eggs on a beach in Guyana that is composed entirely of broken sea shells. Penyapol (1958) has stated that green turtles nest on different types of sandy beaches in Thailand. On the other hand, Hendrickson and Balasingham (1966) found that in Malaysia green turtles prefer beaches of fine sand. Nesting beach preferences, or lack thereof, is important information for the turtle farmer who must get his turtles to deposit eggs on man-made beaches.

Green turtles have laid eggs on completely artificial beaches in the Seychelles Islands, Hawaiian Islands and on Grand Cayman during the course of pilot farming experiments. Details of the type of sand used are lacking.

The presence or absence of vegetation is not a universal prerequisite for green turtle nesting beaches. Some parts of the rookery at Tortuguero are almost covered with Ipomea, Sesuvium, and Sporobolus, and the green turtles nesting in eastern Australia seem to prefer the older, more vegetated cays. The beaches on the Sarawak Turtle Islands are devoid of vegetation, while on the west Malaysian Islands pioneer plants do invade the nesting area. There are some plants on the Aves Island strand, but only scattered clumps of vegetation on the big Southern Yemen rookeries. There are virtually no plants on the nesting beaches on Ascension Island. In Australia, Bustard and Greenham (1969) found that shrubs and trees on the nesting beaches may serve as a cue to the initiation of hole-digging since a majority of turtles studied commenced digging a body-pit in close proximity to these forms of vegetation. This behaviour has adaptive value since the presence of rootlets and/or moisture prevents sand slippage during the construction of the egg chamber.

Green turtles nesting in Surinam appear to be very plastic in their beach preferences since the beaches there are continuously changing in physical structure and location (Schulz, 1964, 1969).

Some of the beaches in the Philippine Turtle Islands are becoming unfit for nesting due to excess accumulation of logs, uprooted trees, roots of coconut palms and other debris cast ashore (Domantay, 1952-53). Similarly, the strand vegetation is encroaching upon some of the nesting beaches in Western Samoa (Hirth, MS).

The cues that green turtles use in selecting their nesting beaches are still unknown. It is well established, however, that the same nesting beaches are used year after year. For example, no adult turtle tagged at Tortuguero has been retaken nesting anywhere else except at Tortuguero. It is also possible that hatchlings are somehow imprinted with some sensible essence of the beach on which they hatch (Koch, Carr, Ehrenfeld, 1969) and that it is detection of this that guides them back to the same beach when they return as reproductively mature females ready to nest. This imprinting trait is also the rationale behind the restocking programme in the Caribbean (see section 6.5).

One of the biggest nesting concentrations of green turtles in the world and the site of extensive ethoecological research is the beach near Tortuguero on the Caribbean coast of Costa Rica. The nesting beach is approximately 38 kilometres in extent and has been described by Carr (1956), Carr and Giovannoli (1957), Carr and Ogren (1959, 1960), Carr and Hirth (1962), Hirth (1963), Carr, Hirth and Ogren (1966), Carr (1967b) and Stubbs (1970).

3.17 Eggs

Green turtle eggs are spherical and white. During oviposition the eggs are usually dropped one, two or three at a time. Most eggs are covered with mucous when they leave the cloaca. Egg laying takes about ten minutes. Freshly laid eggs in Sarawak weigh 36 g each (range 28.6-44.7) and those in Southern Yemen weigh 40.4 g (range 30-44). The average diameter of green turtle eggs ranges from 40 mm in Sarawak (Hendrickson, 1958) to 54.6 mm on Ascension Island (Carr and Hirth, 1962). Eggs on the Tortuguero and Southern Yemeni beaches average between 42 and 46 mm (Carr and Hirth, 1962; Hirth and Carr, 1970). A few abnormally small or non-spherical eggs are usually found in each clutch.

If we assume that the average green turtle weighs about 125 kg (wet weight), that she lays 550 eggs per season and that each egg weighs 38 g, then we can conclude that the average adult female produces about 21 kg of eggs per season, or an amount equivalent to about 17% of her own body weight.

Penyapol (1958) has analysed the nutritive value of green turtle eggs. He found that ash accounted for 1.11% of 100 g of turtle eggs. Based upon the same sample size, he recorded the following major constituents: moisture (79.03 g), protein (11.8 g), phosphorus (227.85 mg), calcium (93.58 mg) and iron (1.95 mg). The caloric content of the 100 g sample was 121.36 (compared to 146 in hen's egg and 189 in duck's egg). Vitamins B_1 and B_2 registered 453 and 442 micrograms, respectively. The total edible portion of the sample was figured to be 92.8%.

Man eats the eggs of green turtles chiefly for their protein content; occasionally local demand is based on a belief that they are an aphrodisiac.

Green turtle eggs are eaten by a variety of predators (Table VI). As the table indicates, feral dogs take a large number of turtle eggs. Humans, of course, take more eggs than any other predator.

Racoons are a terrible menace to loggerhead eggs on the Florida coast and may be preventing rehabilitation of green turtle rookeries there (Carr, pers. comm.).

On high-density nesting beaches, such as Heron Island, Europa Island, and the Sarawak Turtle Islands, nesting females may destroy incubating clutches as a consequence of digging their own nests (see section 4.5).

3.2 Embryonic and hatchling phase

3.21 Embryonic phase

Domantay (1968) has documented the embryology of the green turtle from the time the egg leaves the ovary to the day of hatching. His observations were made in the Philippine Islands where incubation lasts about 50 days. According to Domantay, the early stages of

TABLE VI

Predation on Green Turtle Eggs

Locality	Predator	Authority
	WESTERN HEMISPHERE	
Tortuguero, Costa Rica	dogs, buzzards, opossums, pigs, white-lipped pecoary, coatimundi	Carr, 1956, 1967b
Galâpagos Is.	feral dogs, pigs	Schmidt and Inger, 1957 P. Pritchard (MS)
	EASTERN HEMISPHERE	
Aldabra Atoll	sand crabs (Brachyura sp.) robber crabs (Birgus latro) ibis, dogs, rats	Honegger, 1967
Southern Yemen	feral dogs, foxes, beach crabs	Hirth and Carr, 1970 Anon, 1967c
West Pakistan	feral dogs, jackals, crows, monitor lizards	Minton, 1966
Malaysia	ghost crabs (Ocypode sp.) monitor lizards (Varanus sp.) rats	Hendrickson, 1958
East Indies	monitor lizards, pigs (Sus barbatus)	Raven, 1946
Philippine Islands	dogs, monitor lizards	Domantay, 1952-53

gastrulation are completed before the egg is laid; by the end of the fifth day the neural tube is differentiated into the brain and spinal cord; differentiation of the heart and gut begin about the eighth day; the nervous, digestive and circulatory systems are fully distinguishable by the eleventh day; at about the seventeenth day the eye is differentiated with a lens and iris and the anlage of the carapace is present and differentiating; the scales are fully formed and pigmented by the thirty-first day; two days before hatching the yolk measures about 30 mm in diameter. According to Domantay it takes the hatchlings at least three days to reach the surface.

Penyapol (1958) found that embryos from the Thailand rookeries have a carapace length of about 5, 11.2 and 36 mm on days 14, 20 and 36, respectively; that over the same period the width of the carapace varies from 4 to 31 mm; and, that the forelimbs grow faster than the hindlimbs after day 16.

Deraniyagala (1939) recorded that a 16-day-old Ceylonese embryo has a carapace length of 11 mm and a carapace width of 6 mm. At the same time, the lengths of the fore flippers and hind flippers are 3.5 and 3.0 mm, respectively. Between 29 and 36 days of age, the lengths of the carapace and flippers almost double, and by the thirty-sixth day the carapace is pigmented (dark olive). According to Moorhouse (1933) all traces of the umbilicus disappear at about three weeks of age.

A rather old but comprehensive monograph on embryology, especially that of the head, has been written by Parker (1880).

Agassiz (1857) described in detail the embryology of various turtles, mostly Chrysemys and Chelydra. It would be interesting to compare the embryology of green turtles with those described in Agassiz's classic work.

Bustard, Simkiss, Jenkins and Taylor (1969) have shown that the eggshell is the major source of calcium for developing embryos.

The new hatchling cuts through its eggshell with the aid of a horny protuberance, sometimes called the egg-caruncle, on the tip of its snout. This caruncle disappears after a few days.

3.22 Hatchling period (behaviour, predators and survivorship)

The dorsum of the hatchling is black or dark brownish black or dark greenish black and the edges of the carapace and flippers are usually white; the venter is white except the ends of the flippers which are black but edged with white (see Fig. 8). Sizes of hatchlings are given in Table VII. A picture of a hatchling just breaking through the eggshell is provided by Carr (1967c). Albino hatchlings have been reported from Sarawak (Harrisson, 1963) and from Costa Rica (Carr, 1967b).

TABLE VII

Sizes of one-day-old hatchlings from three different nesting populations (from Carr and Hirth, 1962; and Hirth and Carr, 1970). Values represent the mean and range and are given in millimetres. A hatchling from Southern Yemen weighs about 23 g (range 20-28 in sample of 20).

	Tortuguero N=100	Ascension N=100	S. Yemen N=20
Length of carapace	49.7(46.0-56.0)	51.7(49.1-55.0)	46.9(44.0-48.4)
Width of carapace	38.5(35.0-48.2)	41.6(38.0-48.0)	33.5(31.2-37.5)
Length of plastron	40.0(33.5-46.1)	42.6(38.2-48.1)	36.8(32.8-40.6)
Width of head	15.2(13.0-17.2)	17.0(15.5-20.5)	14.2(12.5-15.6)

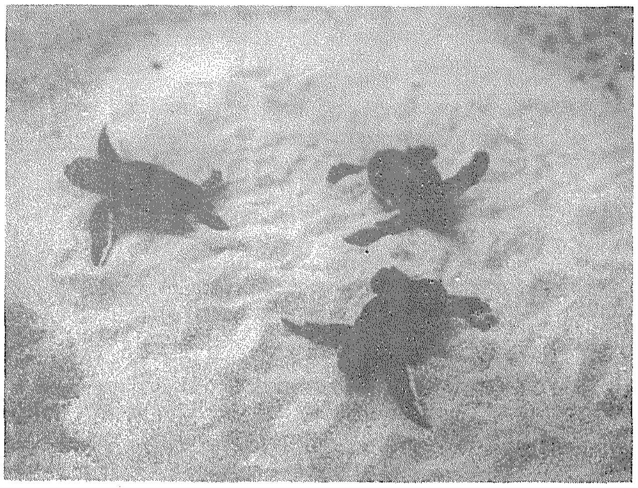

Fig. 8 One-hour old green turtle hatchlings, each about 23 g. The dark carapace and flippers, edged with white, are typical of the species.

The movements of hatchlings can conveniently be divided into the following categories (from Carr and Ogren, 1960): (1) from nest to surface, (2) from nest to wave-wet sand, (3) across wave-wet sand, (4) through wave-wash, (5) through breakers, and (6) travel by hatchlings and immature stages (also see sections 3.51 and 3.53). Phases (1) and (2) above have been the most intensively studied, while virtually nothing is known about the last phase listed above.

The movement from the nest to the surface is a combination of negative geotaxis and allelomimetic behaviour. Hendrickson (1958), Carr and Ogren (1960) and Carr and Hirth (1961) provide detailed accounts of the complex series of activities that characterize the emergence process - the salient feature being that turtles in a nest are not completely independent individuals, but are sort of a super-organism, composed of collaborating hatchlings whose combined efforts carry the "roomful" of individuals to the surface. The climb to the surface usually takes between three and seven days. Emergence from the sand usually takes place at night. Sometimes the entire complement emerges at the same time, while on other occasions the hatchlings emerge in small lots, over a period of 24-72 hours. This is probably due to subdivision of the group by differences in hatching schedules. Turtles hatching singly have reduced prospects of emerging from the nest, and even less chance of reaching the sea.

Hendrickson (1958) believes that some innate mechanism prevents hatchlings from emerging on the surface during the heat of the day. He postulates that if they encounter sand temperatures much above 33°C, they cease activity and resume climbing only when nightfall brings lower sand surface temperatures. Bustard (1967b) found that the majority of Australian hatchlings also emerge from the underground nest at night and he suggests that inactivity during the day of the "lead" turtles near the surface has a dampening effect on the activity of those below—thus ensuring that emergence does not take place when air or sand surface temperatures could be lethal. Mrosovsky (1968) concluded thermal inhibition of activity is a major factor in limiting the emergence of hatchling green turtles to nocturnal hours. Activity is slowed down when sand temperatures rise above 28.5°C.

The advantages of emerging at night are chiefly two: (1) it eliminates exposure to hot sand surface temperatures which could be lethal or which could slow down the turtle in its crawl to the sea and thus lengthen its exposure to predators, (2) it eliminates exposure to diurnal predators.

Hatchlings crawl along the sand surface using their four flippers in typical reptilian fashion (front member moved in conjunction with hind member on opposite side), while adults on shore heave themselves along using sometimes only the front flippers simultaneously and sometimes all four limbs simultaneously.

Carr and Ogren (1960) conducted a series of tests to elucidate the orientation (= the taking up of a direction in relation to a stimulus) of the hatchlings from the nest to the sea. They concluded that the fundamental goal sense involved visual stimuli, and that the response is a modified phototaxis. The "openness of outlook" of a sea-sky horizon will draw them away from a sun or moon when either is over the land. But this relationship between intensity and area is evidently reversed in the case of very bright light. Moorhouse (1933), for example, stated that he could entice the hatchlings back onto the beach after they had entered the sea by shining a bright light. Carr and Ogren (1959) found that they could draw hatchling leatherbacks back to shore after they had entered the surf by setting a kerosene lamp on the shore or by shining a flashlight on them. And, evidently the combined effects of illuminated sky over cities and bright street lights account for the destruction of loggerheads (Caretta caretta) on the coastal highways of Florida (McFarlane, 1963). Mrosovsky (1970) has stated that any kind of visual stimulus has some effect on the seafinding orientation of hatchlings and that under some circumstances the sun or moon could distract hatchlings from the shortest route to the sea and thus increase exposure time to predators. Although the problem is not completely resolved, Mrosovsky (1970) states that the distraction to very bright light is counterbalanced by a behavioural mechanism known as tropotaxis (= simultaneous comparison of intensities on the two sides, and orientation according to the balance thus struck) which ensures that hatchlings will reach the water under almost all conditions.

The sea-finding ability of hatchlings as well as adult females has been further studied on the Tortuguero beach by Ehrenfeld and Carr (1967) and Ehrenfeld (1967, 1968). Spectacles containing special filters were fitted to the heads of adults, and hatchlings were tested in a circular arena where the view of the horizon was unobstructed or where it was blocked by a low wall. They substantiated the claim of others that the water-finding orientation is primarily a visual process (based on brightness rather than colour) and that it involves an appraisal of beach topography. They also concluded that there was no innate compass direction based on celestial cues, although Fischer (1964) did find a fixed direction preference related to the position of the sun in hatchlings tested in a water arena.

In regard to the visual acuity of marine turtles, Walls (1963) stated that "the female marine turtle is in a bad way visually when she comes ashore to lay her eggs at night, for her aerial vision must be hazy and dim even if the moon is bright". Walls describes the anatomy, accomodation, optic axes and other aspects of the chelonian eye. Ehrenfeld (1967) established that green turtles are very myopic when their eyes are out of water. Nevertheless, as described above, vision is indispensable for orientation on land.

Retinal oil globules in C.m. mydas have been examined by Granda and Haden (1970). The areal distribution shows a mean total of 7,803 for orange, 8,460 for yellow and 4,132 for colourless. The apparent lack of areal differentiation is correlated with its marine niche.

Mrosovsky and Carr (1967) examined light preferences of hatchlings in a simple apparatus on the natural nesting beach and discovered that when given a two-choice situation, they prefer blue and green stimuli over red. Light preferences were analyzed further by Mrosovsky (1967) and by Mrosovsky and Shettleworth (1968), and it was found that while wavelength preferences of hatchlings are controlled largely by brightness, the existence of some colour preference cannot be ruled out. Ernst and Hamilton (1969) postulate that turtles with some nocturnal habits prefer the shorter wavelengths of light and that diurnal species prefer the longer wavelengths.

In summary, it has been shown that a brightness preference (at the level of the horizon), a tropotactic reaction to light and the association of the open horizon with the seaward direction could explain the sea-finding orientation of hatchlings, at least on the Caribbean beaches.

Lab-reared yearlings retain the ability to find the sea and even cross complex terrain to reach it, and adult males evidently possess the same ability, although once reaching the surf as hatchlings, they never return to a terrestrial environment except perhaps to bask (Carr and Hirth, 1962). After conducting a variety of experiments with C.m. carrinegra in the Gulf of California, Caldwell and Caldwell (1962) concluded that the sea approach ability is present in both sexes of all ages.

As already mentioned, the habits of the hatchling after it enters the sea are completely unknown. Carr (1967b, 1969c) postulates that the hatchlings are pelagic for some months because observations on captive hatchlings suggest that they have trouble feeding on the bottom in deep water and that their counter-shading (i.e., dark dorsum: white venter) resembles pelagic fish. Many marine organisms are pelagic during the early stages of their life. Carr suggests that the Sargasso Sea might be one place to look for young turtles, especially since they have not been seen in shore-waters anywhere. It is also postulated that hatchlings are carnivorous (in captivity they readily eat a variety of animal food). Theoretically, the sea-air interface would be an optimal niche for a small, weak-swimming, air-breathing, carnivorous animal. Hughes (1969a) believes that loggerhead hatchlings are pelagic and that their movements are regulated to a large extent by dominant surface currents.

Bustard (1970a) states that the black carapace plays an important role in elevating the hatchling's body temperature when it floats on the surface of the sea. He also recorded that hatchlings start to dive regularly at about two to three months of age when they weigh about 1,200 g.

Mrosovsky and Shettleworth (1968) suggest that the temperature of currents off the nesting grounds may partly determine to what extent hatchlings swim or remain planktonic.

Caldwell (1969) cites records of hatchlings being dipnetted off their rookeries in the Revillagigedo Islands and off the coast of Michoacan, Mexico. How long hatchlings remain in these offshore waters is unknown.

Predators of hatchlings are given in Table VIII. As the table shows, hatchlings are taken by a variety of avian, terrestrial and marine predators.

A hypothetical survivorship curve (Fig. 9) indicates the greatest mortality takes place in the very early months of life. It has been estimated that only 2-3% of the hatchlings survive to adulthood (Banks, 1937). It may be as low as 1%.

TABLE VIII

Predation on Green Turtle Hatchlings

Locality	Predator	Authority
	WESTERN HEMISPHERE	
Tortuguero, Costa Rica	buzzards, dogs, jackfish, kingfish, snook, sharks	Carr, 1956, 1967b
Gulf Coast of Mexico	dogs, hogs, crabs, birds, fish, sharks	Mexico, 1966
Pacific Coast of Mexico	raccoons, hogs, dogs, crabs, fish, sharks	Mexico, 1966
Galâpagos Is.	feral cats, night herons, frigate birds, ghost crabs, groupers	P. Pritchard (MS)
Mopelia, French Polynesia	hermit crabs, sea birds, sharks	Eggleston, 1953
Marshall Is.	Polynesian rat (<u>Rattus exulans</u>) red hermit crabs (<u>Coenobita perlata</u>)	Fosberg, 1969
Fiji Is.	mongoose	Bustard, 1970b
	EASTERN HEMISPHERE	
Ascension Is.	feral cats, rock cod, common jack fish, sharks	Carr and Hirth, 1962
Aldabra Atoll	hermit crabs, robber crabs, rats, frigate bird (<u>Fregata minor aldabrensis</u>), flamingo (<u>Phoenicopterus ruber antiquorum</u>), grey heron (<u>Ardea cinerea</u>), black and white crow (<u>Corvus albus</u>), vara-vara (<u>Lutianus bohar</u>) carangue-les-dents (<u>Caranx ignobilis</u>) sharks, barracuda	Hornell, 1927 Honegger, 1967
Southern Yemen	beach crabs, birds, groupers, sharks	Hirth and Carr, 1970
West Pakistan	crabs, birds, mammals	Minton, 1966
Cocos Is.	ghost crabs	Gibson-Hill, 1950
Malaysia	monitor lizards, rats, ghost crab (<u>Ocypode ceratopthalma</u>), snakes (<u>Boiga dendrophila</u>, <u>Python reticulatus</u>), fish, sharks	Hendrickson, 1958
Heron Is. Australia	ghost crabs, rats, silver gull (<u>Larus novae-hollandiae</u>), black-tipped reef shark (<u>Carcharinus spallanzani</u>)	Moorhouse, 1933 Bustard, 1967a

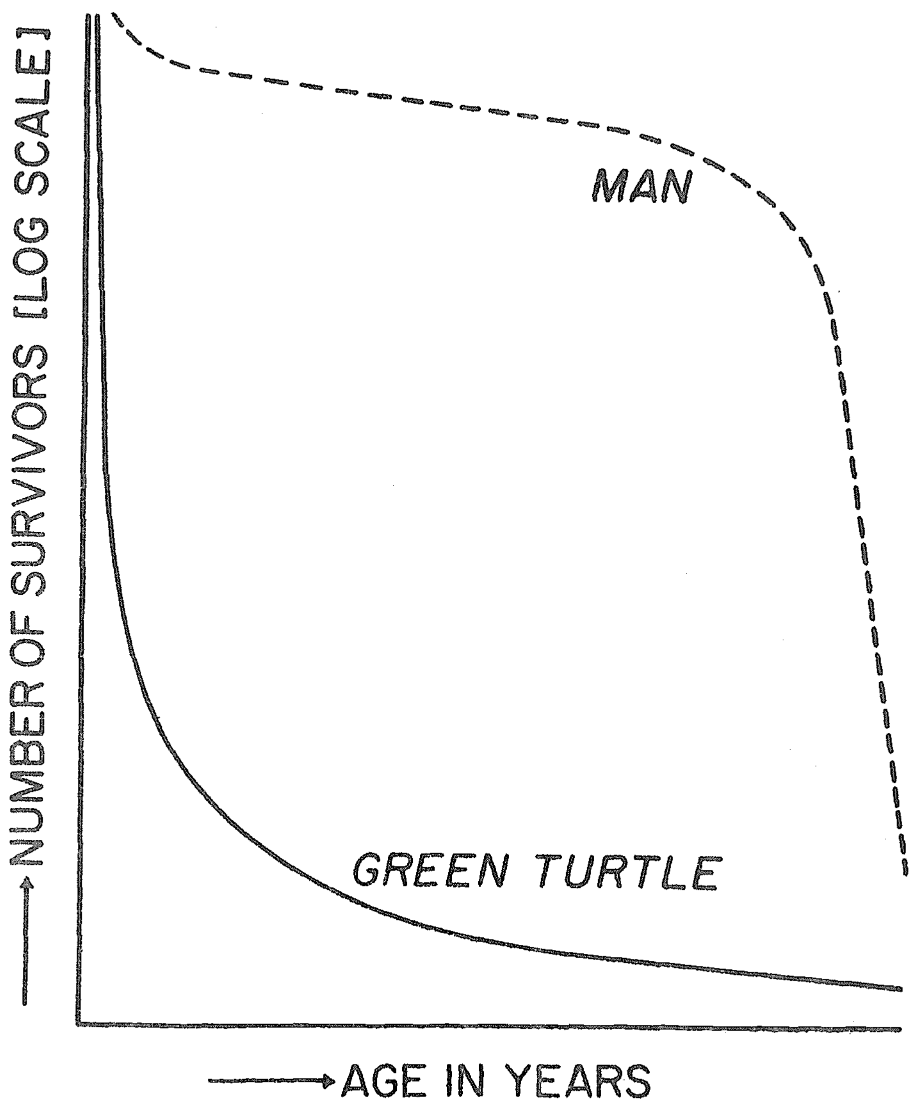

Fig. 9 Hypothetical survivorship curves of green turtle hatchlings a and man. Plotted on the bases of survivors per thousand (log scale) and age in relative units

3.3 Juvenile, sub-adult and adult phase

3.31 Longevity

Little is known about the life span of green turtles in nature. The fact that reproductive maturity may be reached after anywhere from four to 13 years; that some females have been recaptured several times, after two to three years' absence, on their nesting beach; together with observations that predation on adults is minimal (except for man), that epizootics are unknown, and that food is plentiful, all together suggest that adult turtles more than 20 years of age may be common (except in places where they are exploited by man).

Pope (1939) reported that a green turtle from the Pacific Ocean lived for 15 years in the New York Aquarium.

3.32 Hardiness: (see sections 3.13, 3.16, 3,4)

3.33 Competitors

The only known vertebrate competitors of any importance are dugongs, manatees and some herbivorous fish (see section 3.42).

3.34 Predators

Sharks prey upon large green turtles (Moorhouse, 1933; Tinker, 1941; Travis, 1959, 1967; Hendrickson, 1969; Hirth and Carr, 1970). About 4% of adult females observed on Malaysian nesting beaches showed evidences of "assumed" shark damage (Hendrickson, 1958). Groupers are capable of taking individuals up to 4.5 kg (Tinker, 1941). A 22.7 kg green turtle was found inside the stomach of a tiger shark caught near Clarion Island (Beebe, 1937).

Large terrestrial mammals such as feral dogs, tigers and jaguars may take a few adult females as they deposit their eggs on beaches, but such predation is probably minimal.

3.35 Parasites, diseases, injuries and abnormalities

Ingle and Smith (1949) provide a list of references pertaining to the parasites of marine turtles. Their list includes: *Distomum constrictum*, *Ozobranchus branchiatus*, *Stomatolepas transversa*, *Rhytidodoides intestinalis*, *R. similis* and *Platylepas hexastylos*. More recently, other investigators have reported on parasites. Carl (1955) recorded barnacles (*Balanus crenatus*) on the carapace of a sub-adult green turtle found on the coast of British Columbia. Hendrickson (1958) records barnacles (*Chelonibia testudinaria*, *Stephanolepas muricata*) and leeches (*Ozobranchus branchiatus*) on turtles in the South China Sea. He also observed mosquitoes biting the soft skin of the turtle's upper eyelid. Hundreds of barnacles (*Platylepas hexastylos*) encrusted the dorsum and plastron of a sub-adult female taken in Chincoteague Bay, Maryland (Schwartz, 1960). Gupta (1961) took five trematodes from the intestine of a green turtle from Trinidad (*Cricocephalus albus*, *Pleurogonius mehrai*, *Neoctangium travassosi*, *Deuterobaris chelonei* and *Schizamphistomoides chelonei*). Caballero y Caballero (1962) found the trematode, *Orchidasma amphiorchis*, in the intestine of a turtle and Simha and Chattopadhyaya (1969) record a new blood fluke from the heart of a green turtle.

Smith and Coates (1938) describe fibro-epithelial growths in the skin of *mydas* and they discuss the microscopic structure. The growths in wild turtles occur on the neck, eyelids, axillae and groin.

Nothing is known of epizootics among green turtles if, indeed, there are any.

Some individuals may get hopelessly wedged between rocks in their approach to nesting beaches and thereby perish (Carr and Hirth, 1962).

3.4 Nutrition and growth

3.41 Feeding and behaviour on the feeding pastures

Most adults, and to some extent sub-adults, feed chiefly on their grazing pastures (see section 3.42), although in some regions of the world turtles may feed en route between breeding and feeding sites. As far as is known, no feeding, or very little, takes place off the nesting grounds.

The feeding habits of juveniles are not well-known, although it is commonly believed that they are carnivorous for their first few months of life.

It is assumed that some time after the turtle passes one year of age or when it weighs between 1 and 4 kg, it becomes mainly herbivorous (see section 3.42). Whether this dietary shift is gradual or seasonal is unknown. This change in food preference is not uncommon, since it has been reported in other reptiles, especially fresh-water turtles and lizards.

Sizes of grazing males and females on the feeding pastures in the Gulf of Aden are given in Table IX. As is to be expected, the female feeding population includes smaller individuals than the nesting population.

Carr and Carr (1970a) suggest that conditions on the feeding ground may affect the interval between reproductive cycles (see section 3.16).

TABLE IX

Sizes (in centimetres) of green turtles caught on the feeding pastures near Khor Umaira, Southern Yemen (from Hirth and Carr, 1970).

	FEMALES, N=178		MALES, N=112	
	Mean	Range	Mean	Range
Carapace length	88.1	48.3 - 111.8	90.4	71.1 - 104.1
Carapace width	66.8	35.6 - 88.9	68.6	50.8 - 81.3
Plastron length	71.6	38.1 - 86.4	72.9	58.4 - 81.3
Head width	13.7	8.9 - 17.8	14.2	10.2 - 17.8

Travis (1967) observed green turtles on their feeding pastures off the east coast of Somalia and discovered that they "slept" in 30 to 50 minute bouts usually wedged under natural overhangs. He also describes catching sea turtles with remoras.

Carr and Ogren (1960) state that the green turtles in the Caribbean usually spend the night on the bottom, or among rock or coral crags, and that suitable sleeping sites may be located some distance away from their feeding pasture.

Parrish (1958) observed that, in captivity, a resting turtle surfaces for air every 10-56 minutes. Active turtles surface every 30 seconds to ten minutes. Surfacing for air at night usually occurs about every 35-45 minutes. Green turtles slept resting on the bottom of the seaquarium and sleeping began at sundown and lasted all night. Walker (1959) observed that nostrils of green turtles are closed when they rest in an aquarium and he suggests that the closure is an adaptation to prevent water from entering or air leaving the respiratory passages when the animal is resting.

Observations were made on several large C.m. carrinegra in captivity (Caldwell and Caldwell, 1962) and it was recorded that they slept on the bottom of the aquarium with the eyes tightly shut during the night, but nighttime sleep was interrupted by fairly frequent (at least once an hour) trips to the surface to breathe. Presumably the same behaviour takes place in nature on the feeding pastures. However, turtles have been reported feeding at night in the grazing pastures in the Gulf of Aden (Hirth and Carr, 1970).

Sleeping habits of the hatchlings are quite different. They usually float on the surface with their front flippers drawn in along each side of the carapace. Some float with their front flippers extended at right angles to the carapace.

Carr (1967c) postulates that green turtles rarely dive deeper than 12 fm. Most of the best turtle grass pastures are within this limit.

A brief discussion of some of the physiological problems encountered by diving turtles is discussed in Gans and Gaunt (1969). In laboratory tests Berkson (1966) was able to show that metabolic rates are much reduced in prolonged diving and that the green turtle must be very resistant to asphyxial distress. Later, Berkson (1967) found that when the green turtle is subjected to hydrostatic pressure as great as 19 atm., as long as nine minutes may elapse between heart beats. He also measured nitrogen tension in carotid artery blood and in tracheal air and found that equilibrium conditions are never attained during a prolonged deep dive, but that enough nitrogen enters the blood to render the green turtle susceptible to gas emboli in the brain after emergence.

McCutcheon (1947) reported that the specific oxygen affinity of an adult green turtle is 19.0, compared to 28.5 for that of a loggerhead and to 12.0 for that of a box turtle (Terrapene). The differences in the unloading capacity of oxygen are correlated with behaviour and habitat.

3.42 Food and feeding associates

Some food items of adult green turtles are listed in Table X. As the list indicates, adult turtles are mainly herbivorous but they are not averse to eating animals. In fact, captive turtles are commonly fed animal food (section 3.43).

Other investigators have reported on the feeding habits of the green turtle but their accounts are of a general nature or they have not given the exact feeding site or they have reported on only one or two individuals. These works follow: Zostera along the Atlantic coast (Kingsley, 1885); algae and Zostera (Gadow, 1909); Cymodocea, Thalassia, Zostera and Halophila

TABLE X

Food of Mature Green Turtles

Locality	Food	Authority
	WESTERN HEMISPHERE	
Bermuda	*Zostera*	Babcock, 1937
Florida	*Sagittaria*, *Vallisneria*, *Thalassia*, *Cymodocea*, jellyfish.	Neill, 1958 Carr and Caldwell, 1956
West Indies	*Thalassia*, molluscs, crustacea	Underwood, 1951
Gulf Coast of Mexico	*Cymodocea*, *Thalassia*	Mexico, 1966
Mosquito Cay, Nicaragua	*Cymodocea*, *Thalassia*	Carr, 1954
Ceara, Brazil	algae (Rhodophyceae, Chlorophyceae, Phaeophyceae), *Deplanthera*, molluscs, oscidians, sponges, bryozoans, crustaceans, echinoderms	Ferreira, 1968
Pacific Coast of Mexico	algae (*Gelidium*, *Sargassum*, *Rhodymenia*, *Gracilaria*, *Griffitsia*, *Liagora*, *Ulva*, *Gratelonpia*), *Cymodocea*, *Thalassia*	Carr, 1961 Anon, 1966 R. Marquez, Pers. comm.
Chile	*Zostera?*, alga, sponges	Yanez, 1951 Donoso-Barros, 1966
Galápagos	algae (*Caulerpa*), mangrove roots and shoots	P. Pritchard (MS)
Maui, Hawaii	green algae	Hirth (MS)
Tonga Is.	*Halodule*, *Halophila*, *Syringodium*	Hirth (MS)
Fiji Is.	red and green algae, *Syringodium*	Hirth (MS)
Kermadec Is.	*Pterocladia capillacea*	Oliver, 1910
	EASTERN HEMISPHERE	
Seychelles Is.	*Cymodocea*	Hornell, 1927
Gulf of Aden	*Posidonia* (or *Enhalus*), *Halodule*, brown and red algae	Hirth and Carr, 1970
Krusadai Is.	algae (*Gracillaria*, *Sargassum*), *Cymodocea*	Kuriyan, 1950
Ceylon	*Cymodocea*, *Thalassia*, *Halophila*, algae	Deraniyagala, 1939, 1953
Sulu Sea	green algae and *Sargassum*	Domantay, 1952-53
Great Barrier Reef	sea grasses	Yonge, 1930

(Ingle and Smith, 1949); plant matter, crabs, ascidians and barnacles in gut of one individual taken off South Africa (Hughes, Bass and Mentis, 1967); algae in the South Seas (Roedelberger and Groschoff, 1967); eelgrass, algae, crabs and snails (Schwartz, 1967); and, animal food such as sponges, Pteropods and jellyfish (Brongersma, 1967).

Pieces of plastic have been found in the stomachs of turtles taken in the South Pacific (Hirth, MS) and in turtles captured off the Pacific coast of Costa Rica (Carr, pers. comm.).

One of the best described feeding pastures is found near Khor Umaira, Southern Yemen (FAO, 1968; Hirth and Carr, 1970). Here the densities of turtle grass reach 2,500 leaves per m^2. The stomach of six mature turtles packed solidly with two species of turtle grass weighed between 1.8 and 2.5 kg. Unfortunately, information on assimilation is lacking. Ricker (1969) estimates that the K value for marine herbivores would rarely exceed 15%. K is defined as the growth coefficient, or the turtle's annual increment of weight divided by the quantity of food it has consumed.

In terms of primary organic production, the Western Indian Ocean is a region of contrast, containing some of the richest and some of the most infertile waters in the world. Although measurements have not been made along the Somali coast where good green turtle pastures are found, the region has been assigned a moderately high level of production (.26.50 gCm^{-2} day^{-1}) and it is possible that much higher levels occur (Ryther *et al.*, 1966). Primary and secondary productivity studies are greatly needed, especially on the feeding grounds, but it may be that feeding experiments in captivity are the only practical way to elucidate energy flow in the relatively simple sun-grass-turtle food chain.

Burkholder, Burkholder and Rivero (1959) obtained some quantitative and qualitative data on turtle grass, Thalassia testudinum, in the West Indies. Among other things, they reported a biomass (dry weight) of 5.66 kg/m^2, of which 80 to 90% was underground; and, that the leaves contained about 13% protein, 25% ash, 36% carbohydrates, 16% crude fibre and 0.5% fat. More studies like this are needed.

C. den Hartog (1970) has written an interesting monograph on the sea grasses of the world. In many instances the distribution of green turtles coincides with the distribution of sea grasses, and certainly a century ago the fit was even closer (see Fig. 10).

Marine turtles and sirenians are probably the only big vertebrates grazing the extensive marine

Fig. 10 Underwater photo of Syringodium isoetifolium, a marine angiosperm, near the Fiji Islands. This is a favourite food of herbivorous sub-adult and adult green turtles in some areas of the Southwest Pacific Ocean

pastures, and competition between these groups is probably minimal. In the West Indies, Randall (1965) found parrotfishes (Scarus and Sparisoma), surgeonfish (Acanthurus), echinoids (Lytechinus, Tripneustes and Diadema), and the green conch (Strombus gigas) competing with the green turtle for marine grasses (Thalassia and Cymodocea). Stomach analyses of balahoo fishes, Hemiramphus brasiliensis, in the West Indies showed their main food to be leaves of Thalassia (Burkholder, Burkholder and Rivero, 1959). Banner and Randall (1952) wrote about the invertebrate life in a turtle grass area around an atoll in the Gilbert Islands and found that even invertebrates were scarce. According to Wiens (1962) the turtle grass (Thalassia) around some of the Pacific atolls rarely grows over 0.3 m high but it makes dense stands over surfaces of sand in which its creeping rhizomes form an interwoven mat. He also found that turtle grass may be the dominant vegetation in lagoons from zero tide level to a depth of 1.6 fm.

3.43 Growth rate

Rates of growth under natural conditions are relatively unknown, although estimations have appeared in the published literature. As long ago as 1916, Schmidt stated in regard to the Caribbean turtle fisheries that "the most important facts to be determined are the rate of growth of turtles and their migrations". While some good information on movements of turtles in some parts of the Caribbean is now available, there is still a dearth of good empirical data on growth rates. During the course of his pioneer studies on growth rates in Caribbean turtles, Schmidt found that nine turtles initially weighing between 2.3 and 20 kg showed weight increases of from 138 to 430 g per month after 3.5 to 11 months in the ocean. His findings also suggest that green turtles weighing about 2.3, 5.5 and 9.1 kg are about 1-1.5, 2-2.5 and 3-3.5 years old, respectively. He further postulated that a one-year-old green turtle is about 27 cm in length and a two-year-old is about 35 cm long. Moorhouse (1933) estimated that one-year-old turtles are 20.3 cm long. Ingle and Smith (1949) state that growth rate in early years is about 3.2 kg or 17.8 cm in carapace length per year. One-year-old turtles weigh between 1.8 and 3.6 kg according to Parsons (1962). Carr (1967c) believes that turtles weigh between 0.9 and 2.3 kg when they are one-year-old. Australian green turtles weigh about 22 g at birth and about 1,200 g two to three months later (Bustard, 1970a).

Carr and Caldwell (1956) relate how an Atlantic green turtle weighed 20 kg at time of capture and then weighed 2.7 kg more when it was recaptured 102 days later. Other gains were 0.03 cm per day in carapace length and 0.01 cm per day in width of carapace.

Witham and Carr (1968) report that a yearling released when weighing about 830 g was recaptured 30 months later some 65 nautical miles from the release site and weighed 6,350 g. This recapture was of further significance because the individual was a pen-reared turtle and the fact that it was recaptured is some evidence that pen-reared animals may be able to adapt to the normal ecologic regimen of the species after a year in captivity.

Hendrickson (1958) postulated that there is no marked decrease in rate of growth until the animal reaches maturity and that maturity is attained in four to six years. On the other hand, Caldwell (1962c) theorized that there is a marked decrease in growth rate after about the first three years and that tropical turtles require at least eight years to reach maturity. More recently Carr and Goodman (1970) have shown that after reaching reproductive maturity, female green turtles at Tortuguero, Costa Rica grow only about 0.25 cm per year in carapace length and width (see Fig. 11). According to Carr and Goodman, "It now appears that some green turtles mature at small, and others at large sizes, and that once they mature – that is, once they have made their first trip to the nesting beach – their growth becomes negligible".

These data suggest that the growth of green turtles is similar to most other animals, i.e., characterized by a sigmoid growth curve.

Working in the Gulf of Aden, Hirth and Carr (1970) found no significant differences between weights of females and males of the same length. The same authors compared the weights of turtles from different populations and found that female turtles from Southern Yemen are heavier than those of similar lengths in the South China Sea; and while the weights of the larger females from Yemen are similar to the Caribbean green turtles, they weigh somewhat less than the Atlantic green turtles on Ascension Island. A generalized weight-length curve is provided in Fig. 7. Generally speaking, the weight of a green turtle at reproductive maturity will be five thousand times greater than its weight at hatching.

The weights of mature females in Surinam with carapace lengths of from 100 to 122 cm vary from 121 to 224 kg (Pritchard, 1969). The average weight of a mature female from Tortuguero, Costa Rica, is about 114 kg and the maximum is about 159 kg (Parsons, 1962).

Caldwell (1962b) noted a tendency for males of C.m. carrinegra to be lighter than females beginning at a carapace length of about 76.2 cm. He also described the relationship between carapace length (L) in inches and weight (W) in kg as follows: $\log W = -2.14 + 2.60 \log L$.

As Fig. 6 indicates, the mean lengths of nesting turtles in the Gulf of Aden, China Sea and Caribbean Sea are similar, while the Guiana and Ascension turtles are probably the world's largest.

The heaviest green turtle reported in the literature weighed 386.4 kg (Carr, 1952). The heaviest reported in recent years was a 241 kg female on Ascension (Carr and Hirth, 1962).

Almost half of the wet weight of a green turtle represents edible protein. Deraniyagala (1939) and Schroeder (1966) respectively state that approximately 41.9% and 40% of the live weight is edible meat.

Ingle and Smith (1949) found that the flippers and meat of a 119 kg male and a 96 kg female constituted 47 and 52% of the total weight respectively. The rest of the weight of the female was distributed as follows: head, 2.4%; tail, 0.24%; neck, 1.7%; kidney, 0.23%; liver, 2.3%; heart, 0.24%; calipee, 6.7%; carapace, 15.5%; and entrails, 10.5%. The weights of 45 and 68 kg females were also distributed in a similar fashion.

A hatchling from the Maldive Islands, fed on fish and bread, weighed 4.4 kg and had a carapace length of 320 mm and a carapace width of 270 mm after about 13 months in captivity (Deraniyagala, 1939). Gibson-Hill (1950) reports that the Malay on the Cocos Islands raise green turtles in captivity and that they reach a length of about 25 cm in one year. Hatchlings kept in semi-captivity in a lagooon in the South Pacific had carapace lengths of from 15 to 20 cm after ten months a diet of kitchen scraps, fish and shellfish (Wiens, 1962). Three green turtles raised in an aquarium grew from about half a kg to about

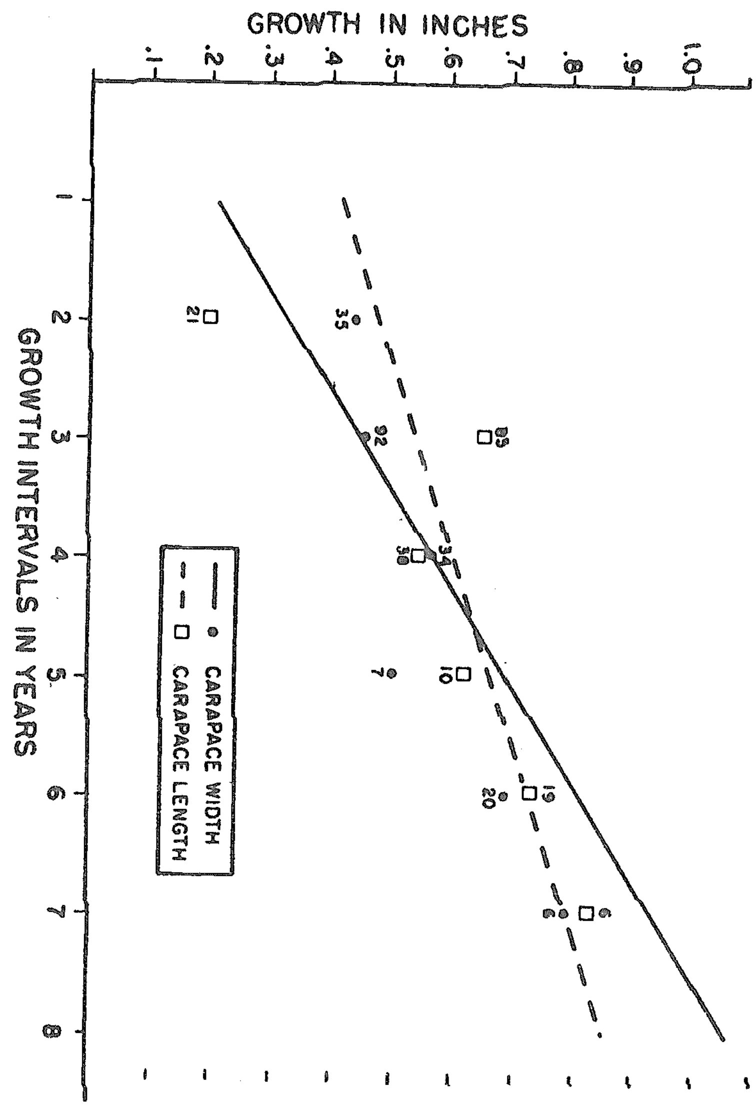

Fig. 11 Growth of mature female, green turtles at Tortuguero, Costa Rica. Squares and circles show mean growth for the corresponding growth interval. Numbers indicate size of samples represented by means. (from Carr and Goodman, 1970; Copyright, 1970, by the American Society of Ichthyologists and Herpetologists)

23 kg in nine and a half years (Flower, 1937). Caldwell (1962c) reported the weight increases of four hatchlings maintained in captivity for three years as follows: the mean weight increase was 135 g the first year, 2,725 g the second year, and 5,000 g the third year. In captivity, hatchling green turtles can grow up to between 22.5 and 25 cm in six months according to Schroeder (1966). Evidently green turtles in captivity readily eat fish and other meat (see also Hornell, 1927; Loveridge, 1945; and Parrish, 1958).

People in the Tuamotu Archipelago have raised hatchlings on coconut meat and fish and they have obtained a length of 50 to 71 cm in 3 to 3½ years. Fishermen on various islands in the Kingdom of Tonga sometimes keep adult turtles in kraals and feed them on turtle grass which washes up on the beach (Hirth, MS).

3.44 Metabolism

Appa Rao and Dutt (1965) examined the chemical composition of muscle of an adult male green turtle. Results indicate that the water content of turtle flesh is close to that of fishes (i.e., 80 g water per 100 g muscle). The fat content (0.76 g per 100 g muscle) is lower than in most fishes. In 100 g of muscle they found 15.35 g protein, 510 mg phosphorus, 210 mg calcium, 34 mg iron, 0.21 mg copper, 0.20 mg cobalt and 0.20 mg molybdenum.

Chiefly because green turtle oil is used for therapeutic purposes in some parts of Mexico (used in treatment of tuberculosis, leprosy, and as a source of vitamins), Giral and Cascajares (1948), Giral, Giral and Giral (1948) and Giral (1955) have begun a study of its chemical properties. Some of the most common fatty acids in the oil are lauric, myristic, palmitic, stearic and palmitoleic. The presence of large amounts of lauric and myristic acids may be characteristic of Chelonia mydas. The sterol of body oil in a green turtle from New Guinea contained 96% cholesterol, 3% B-sitosterol, 0.2% campesterol and 0.15% stigmasterol (Minato and Otomo, 1969).

Biochemical composition and nutrient quality of the flesh may vary among individuals of a population depending on such things as age and sex, stage in the reproductive cycle, kinds of vegetation eaten on the feeding pasture, and physiological stress induced by long-range movements.

Evidently, the flesh (or fat or blood) of some Chelonia is toxic to humans. Halstead (1970) gives a list of references pertaining to sea turtle poisoning. The list contains only one case of poisoning by green turtles and this incident caused 18 deaths in Ceylon in 1840. However, the list also contains other instances of chelonitoxication in which the species was un-unknown. Most reports of chelonitoxication are from the Indo-Pacific region. The origin of turtle poison is unknown but most investigators who have studied the problem appear to be rather consistent in their opinion that the toxin is derived from poisonous marine algae eaten by turtles (see Halstead, 1970 for review of literature; also Boulenger, 1890; Halstead, 1959, 1969; and Taylor, 1970). The symptoms of chelonitoxication vary with the amount of flesh ingested and with the person. Symptoms generally

after eating the meat and initial symptoms include nausea, diarrhea, epigastric pain and vertigo. There are no known antidotes for chelonitoxin. The treatment is symptomatic. Further studies on chelonitoxication and documentation of green turtle cases are needed.

Ammonia is the major end product in the urine of mydas as it is in marine teleostean fishes. The green turtle also excretes a large amount of hippuric acid and this may be due to its herbivorous diet (Khalil, 1947).

An interesting adaptation of Chelonia mydas to its marine environment, pointed out by Schmidt-Nielsen (1959) among others, is its ability to discharge excess salt by means of salt glands located near the eyes. In this regard the green turtle is similar to the marine iguana and sea snakes. When on land, a turtle discharging salt looks as if it is "crying". Carr and Ogren (1960) suggested that the "crying" of nesting females also serves to keep the eyes clean of sand.

Holmes and McBean (1964) have clearly shown that the "salt gland" in mydas is the predominant route of sodium and potassium excretion. They further hypothesize that sea turtles drink sea water not only to obtain osmotically free water but also to enable the excretion of potassium ingested as food. Such information may be important for future turtle farmers in providing the proper milieu for their captives.

Ellis and Abel (1964a, b) describe how the turtle's salt gland tissue is in some ways different from the salt-secreting epithelia of fish and birds. Abel and Ellis (1966) state that histologically the modified lacrymal glands of marine turtles may be classified as compound branched tubular glands and that the salt-secreting nasal glands of marine birds, the rectal glands of elasmobranchs and the lacrymal glands of marine turtles have many common cytochemical and cytological features.

The marine plants that the turtles graze on probably have a salt concentration similar to that of sea water and no doubt the salt gland of the turtle operates in response to this electrolytic load.

Thorson (1968) measured the body water in sub-adult C.m. mydas and C.m. agassizii and determined its apportionment among the major fluid compartments. Both subspecies were similar in having total body water account for about 64% of body weight.

For some aspects of diving physiology, see section 3.41.

3.5 Post-hatchling movements and basking behaviour

3.51 Developmental migrations

Developmental migrations may be a natural part of the life cycle of the green turtle, although little is known about the subject. A non-breeding population ranging in weight from 5 to 52 kg appears on the feeding pastures off the upper west coast of Florida in April and disappears in November (Carr and Caldwell, 1956). This population is made up chiefly of sub-adults and a few juveniles. The Florida pastures may be a stop in the developmental migration of turtles which hatch on the rookeries of Mexico and the Yucatan Peninsula. Sub-adults are also taken between March and November in the state of Sonora, Mexico. Carr (1961) draws a parallel between this Sonoran colony and the fleet of young individuals which appear off the west coast of Florida. Schmidt (1916) may have been describing a developmental migration when he said ,"Whether the green turtle, the species most commonly caught, breeds in the Danish West Indies, or whether it first arrives there as specimens ; 20-30 cm in length is, strangely enough, unknown, and it is a matter of great importance".

An itinerant population of sub-adult green turtles is found near Bermuda and is probably carried there by the Gulf Stream (Mowbray and Caldwell, 1958). A juvenile and sub-adult (lengths 22.5 and 42.5 cm) have been recovered on the beaches of Long Island, N.Y. (Latham, 1969), but apparently were waifs.

3.52 Dispersal and remigrations

Most adult green turtles customarily make seasonal trips between feeding pastures and breeding grounds, and some of these movements may encompass thousands of km (see section 2 and 3.1). Fig. 12 shows some places where adult females have been recovered after having been tagged on their nesting beaches. All the arrows in the figure do not indicate location of feeding pastures, or routes of travel, but they do indicate the magnitude of the spread from three major nesting beaches and thus give an indication of the "total range" of at least some individuals in the population. The two best studied remigration patterns are those of the Tortuguero and Ascension Island colonies.

From 4,200 mature green turtles that have been tagged at the Tortuguero rookery, there have been 175 international recoveries (Carr, 1967c). Most of the recaptures have been made on the feeding pastures off the Nicaraguan coast. One individual was recovered in Trinidad, some 2,400 km from the site of tagging. Two individuals marked on the Tortuguero beach were later taken about 800 km away in Colombia. It was calculated that the minimum speed of travel for one individual over a 34-day period was 23.5 km per day and that the second turtle travelled a minimum of 21.6 km per day over a 37-day period (Carr and Ogren, 1960). It now appears that two main fleets converge upon Tortuguero to nest - one comes from the south (i.e., from Panama and Colombia) and the other from the Miskito Cays and Nicaraguan coast (Carr, 1967b). One of the most amazing facts pieced together from tagging work is that the Tortuguero turtles return to the same segment of beach to nest, after absences of from two to four years (see section 3.16).

Some 556 turtles have been tagged while nesting on Ascension Island and ten have subsequently been recovered on the feeding pastures off Brazil, a dispersal of some 2,240 km (Carr, 1967c). These turtles also show a propensity to return to specific, small beaches on Ascension for nesting (Carr, 1965).

Five females tagged on Musa and Sharma beaches in Southern Yemen have been recaptured on the east coast of Somalia (Hirth and Carr, 1970). Assuming that the turtles swam with the prevailing surface currents, the longest recapture would constitute a movement of about 3,200 km (i.e., from Sharma to Chisimayo around the Gulf of Aden). Minimum rate of travel for two Yemeni green turtles was computed at 22.4 km per day for 85 days.

Pritchard (1969) reported that one green turtle tagged in Surinam was recovered in Brazil after having travelled a distance of about 1,600 km in six weeks. Schulz (1969) also disclosed the recovery of two Surinam turtles in Brazil. It thus appears that the turtle grass pastures off the coast of Brazil are the feeding grounds for two distinct nesting populations, viz., the Ascension Island nesters and the Surinam nesters.

Harrisson (1960) stated that a female tagged at Talang Besar, Sarawak in 1953 was recovered in 1959 in a net off Kimanis, North Borneo. This represented a dispersal of about 800 km.

Hendrickson (1969) reported that two greens tagged on French Frigate Shoals were later recaptured in the main Hawaiian Islands about 800 km ESE; and that two individuals marked at Pearl and Hermes Reef were resighted on French Frigate Shoals - again a movement of about 800 km ESE.

Green turtles tagged on Heron Island,

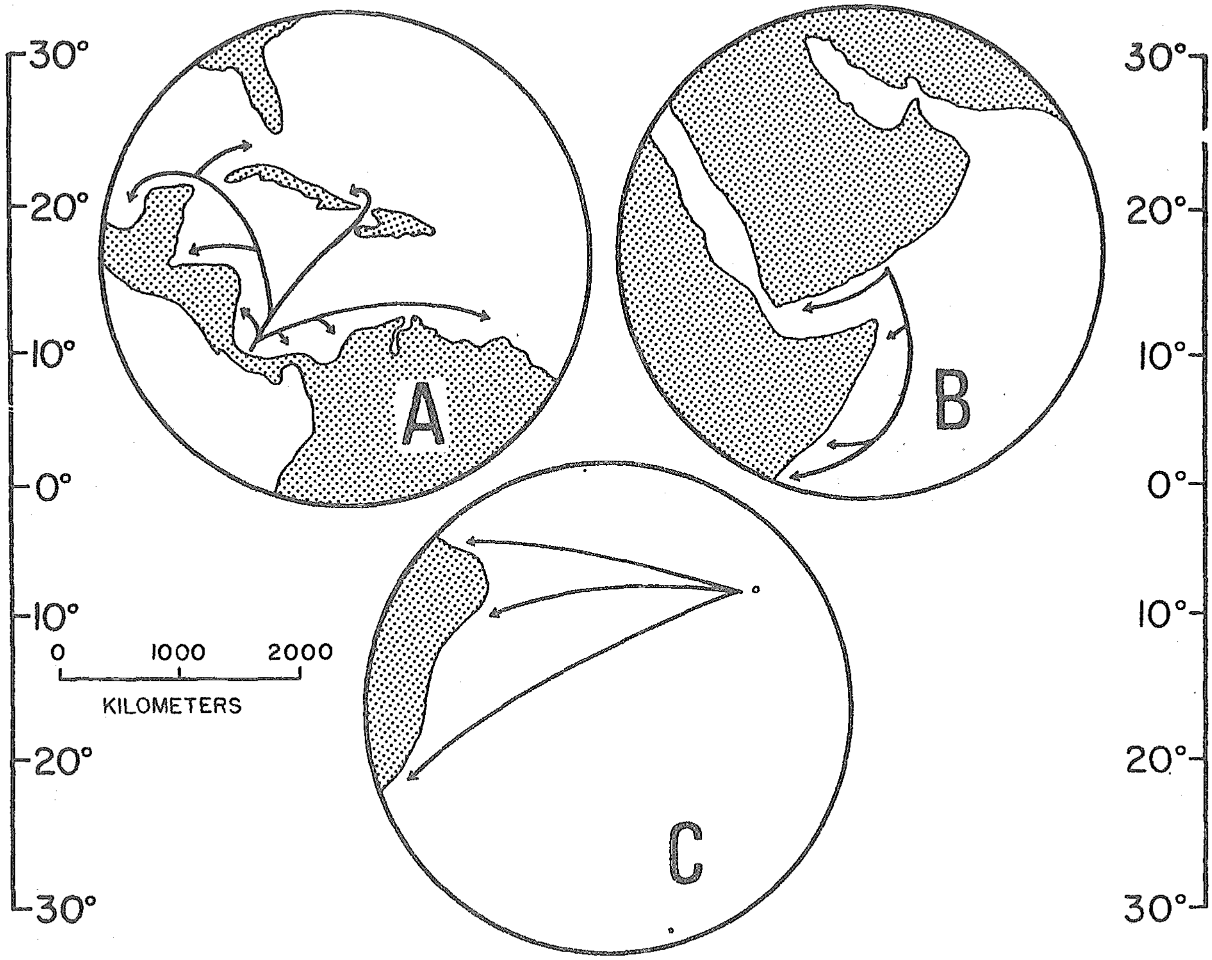

Fig. 12 Long-distance recoveries of green turtles. Arrows indicate spread from the nesting beach and are not intended to suggest routes. A = tagging site was Tortuguero, Costa Rica (adapted from Carr, 1967b); B = tagging site was Musa and Sharma Beaches, Southern Yemen (adapted from Hirth and Carr, 1970); C = tagging site was Ascension Island, South Atlantic (adapted from Carr, 1967b)

Queensland, have been recaptured in Papua and New Caledonia (Bustard, 1969c).

Montoya (1969) found a general movement north along the Mexican coast after oviposition.

It is postulated that the green turtles nesting on the southern atolls of the Seychelles Islands remigrate there from feeding pastures off the East African coast and from the Mozambique Channel, although there have never been any tag recoveries to substantiate this. Large numbers of green turtles, including juveniles, are seen off the beaches in Tongaland, but they do not breed there (Hughes, 1969b).

In some of the earliest tagging experiments, Schmidt (1916) released 65 marked green turtles of various sizes around St. Thomas and St. Jan in the West Indies and recaptured 14% from three to eleven months later. Most recoveries were made just a few kg from sites of release. The longest movement recorded was about 80 km and this individual was recaptured ten months after being tagged. Schmidt concluded that young individuals are rather stationary.

Carr and Sweat (1969) report that a yearling green turtle tagged and released in the lower Florida Keys on 17 October 1967 was retaken on 15 November 1968 off Cape Hatteras, North Carolina.

Oliver (1955) made 23 observations on an adult green turtle as it cruised leisurely in a large salt water stockade and he reported a cruising speed of 1.4 to 2.2 km per hour. Various swimming patterns of captive turtles are further described by Parrish (1958).

3.53 Navigation and orientation

The ability of green turtles to navigate (= ability to initiate and maintain directed movement independently of learned landmarks) across vast expanses of featureless ocean is one of the most intriguing aspects of their biology.

Working with six loggerheads displaced off the Florida coast, Carr (1962a) was able to show that at least the initial movements of some individuals were non-random. In the same paper, Carr discusses the value of telemetry in unravelling the mysteries of open-sea navigation.

The evolution and ramifications of the Ascension-Brazil pattern are discussed by Carr and Hirth (1962) and Carr (1962b, 1964, 1965, 1967a). It is hypothesized that the hatchlings are carried to Brazil by the South Equatorial Current and that for adults returning to the island the shortest route would be directly eastward from the hump of Brazil against the same current. Evidently food would be available for the surface-swimming hatchlings, since according to Walford (1958), the surface waters of at least some branches of the South Equatorial Current are quite fertile. At places where the current diverges, there would also be more nutrient cycling through upwelling. According to Carr (1967b) it would take a hatchling about three weeks to get to Brazil from Ascension.

The Ascension-Brazil pattern may not have originated under present physiographical conditions, but may be an artifact of continental drift. This idea is discussed by Carr (1967a). In this connection, Myers (1967) has found that the fish evidence supports the concept that the final parting of Africa and South America, and hence the origin of the South Atlantic Ocean, took place at some time during the earlier half of the Mesozoic.

Carr (1965) considered celestial navigation as a possible guidance mechanism in long-range movements of the green turtle, but at least bi-coordinate star navigation no longer seems to be a realistic hypothesis in view of the fact that Ehrenfeld and Koch (1967) found the Atlantic green turtle to be extremely myopic when its eyes are out of water. However, other types of navigation involving the sun or moon have not yet been critically evaluated or tested.

Several types of orientation and navigation, with special reference to the Ascension-Brazil remigration, are discussed by Carr (1967b). These include orientation based upon olfactory cues, light-compass sense, magnetic sense, perception of Coriolis force and inertial guidance. He also discusses some of the problems a green turtle would have to overcome in order to navigate using celestial information.

It would be informative to be able to track a "fleet" of green turtles in their movement from the coast of Brazil to Ascension - assuming that they do travel in concert. Future research may show that swimming together improves accuracy of orientation, especially when the goal is an island. Hamilton (1967) has already discussed this idea in relationship to avian remigrations and has postulated that orientation of a flock of birds is more accurate than individual orientation; and that flocking may be helpful to juveniles making the trip for the first time.

Now that some older theories of non-visual navigation have been resurrected (for review, see Griffin, 1969), it would be worthwhile to examine a green turtle's sensitivity to subtle geophysical and oceanographic cues, i.e., forces which separately or synergistically could provide a bi-coordinate grid. A step in this direction has been taken by Koch, Carr and Ehrenfeld (1969). They postulate that olfactory cues emanating from Ascension Island could be recognized by turtles off the Brazilian coast and thus play a part in the Ascension-Brazil remigration. Homing studies are now underway on

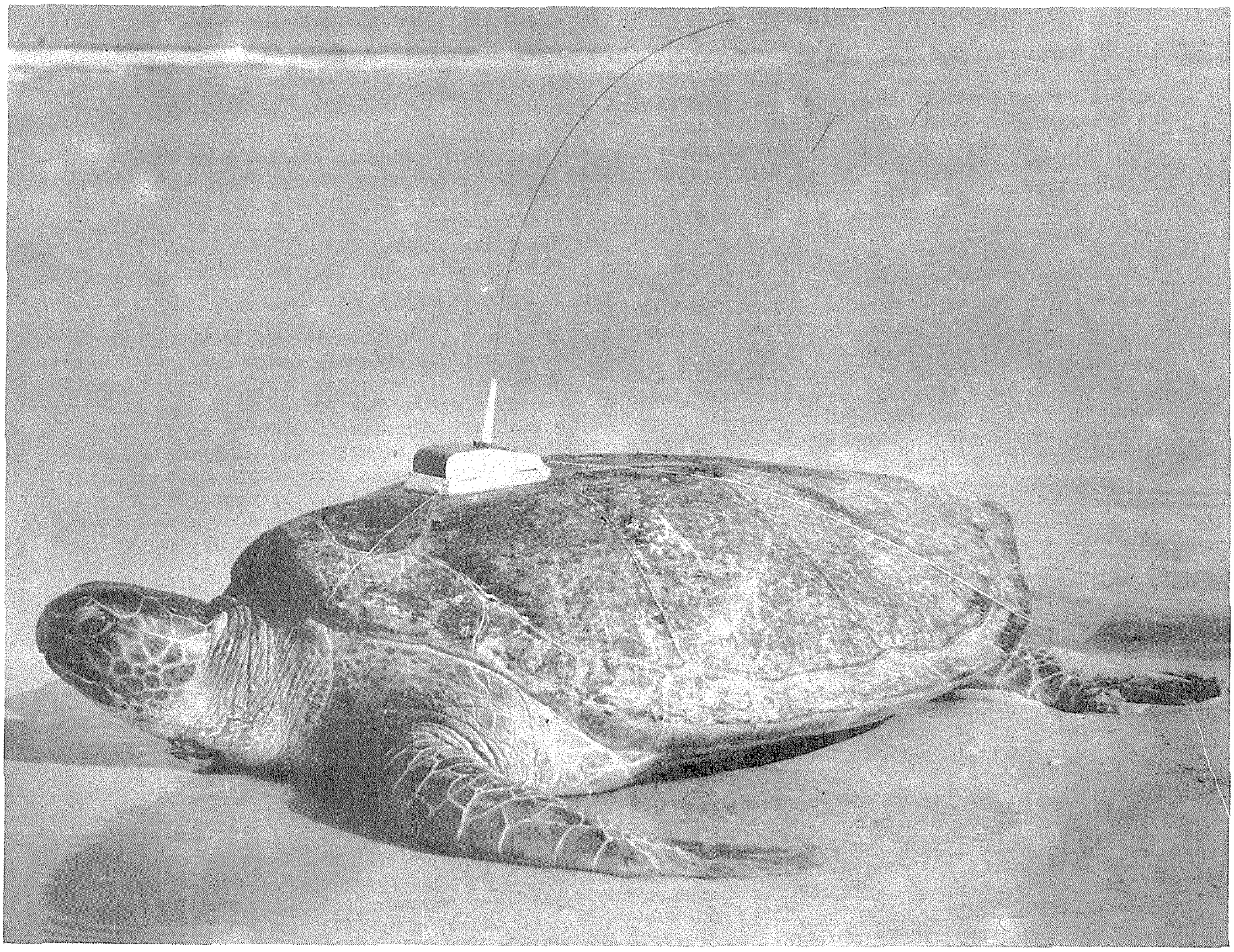

Fig. 13 A radio-equipped green turtle. Such turtles may be useful in tracking movements at sea. In one modification, the turtle tows a float containing the transmitter (photo courtesy A. Carr and Scientific American; see Carr, 1965)

Ascension Island. Preliminary results indicate non-random movements by a turtle out of sight of fixed landmarks (Carr, pers. comm.).

Ridgway et al. (1969) studied sensitivity to sounds in three sub-adult green turtles and they found maximum sensitivity in the region of 300 to 400 Hz. They conclude that the ear is clearly a low-frequency receptor with a useful span of probably 60 to 1,000 Hz, and they further state that "both on land and in the sea, this ear no doubt enables the animal to perceive many important signals". Is it possible that green turtles possess some kind of sonar sense?

It is most likely that turtle navigation is a composite process employing different senses and based upon a multiplicity of cues.

Preliminary attempts at tracking turtles for short distances have been made with floats, balloons and radio-telemetry (see Fig. 13). It may well be that tracking turtles with earth-orbiting satellites will be the only way to follow movements with any great precision.

3.54 Basking

Some Pacific green turtles are known to bask or rest on shore (see Fig. 14). The basking habit has been reported from such widely scattered Pacific localities as Islas Revillagigedo, Hawaiian Leewards and the Galápagos (Mellen, 1925; Wetmore, 1925; Grant, 1927; Carr, 1952; Kenyon and Rice, 1959; Parsons, 1962).

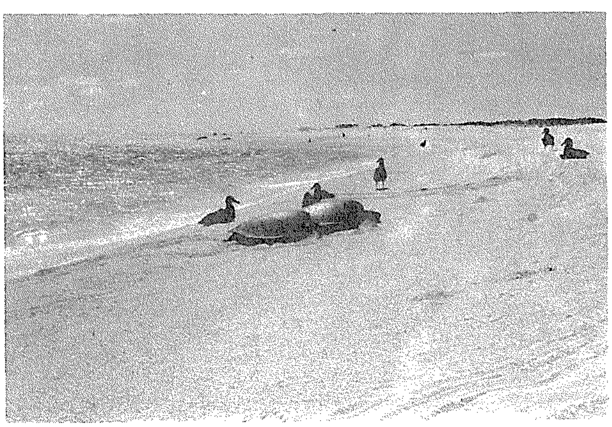

Fig. 14 Basking green turtles in the Hawaiian Leewards (photo, courtesy E. Kridler). Only Pacific turtles are known to bask

Several hypotheses have been offered to explain the basking habit among all kinds of turtles. Cagle (1950), Neill and Allen (1954) and Boyer (1965) suggest that basking might be a form of thermo-regulation, aid ecdysis, free the turtle of ectoparasites or eliminate epizoic algae. Pritchard and Greenhood (1968) suggest that basking aids in the synthesis of Vitamin D. The habit may also aid digestion or it may be a prelude to oviposition (but in the Hawaiian Leewards male green turtles bask too). In the Gulf of Carpentaria female green turtles bask during the mating season (Bustard, MS). It is also possible that basking serves a social function.

In view of the ever-expanding human population (and the quest for food) basking aggregations of green turtles are now at a disadvantage in their struggle for survival. Basking has not been observed in Atlantic green turtle populations. If the habit was not more widespread in earlier years, its occurrence today in some populations and not others may be just behavioural polymorphism.

Green turtles, like all reptiles, are ectotherms. Hirth (1962) found that the cloacal temperatures of adult, female, green turtles at Tortuguero, Costa Rica, upon emerging from the sea for oviposition, were very similar to the sea water temperature (average of turtles 29.9°C; range of sea water temperature 27.5–28.5°C).

4 POPULATION

4.1 Structure

4.11 Sex ratio

Natural sex ratios in green turtle populations are virtually unknown. No studies have been made which elucidate the sex ratios in clutches of hatchlings and virtually nothing is known about sex ratios in the juvenile and sub-adult populations. It is only when larger individuals are caught on the feeding and breeding grounds that biologists are able to glean something of the sex ratios and these data are not entirely accurate.

Hirth and Carr (1970) provide evidence that females outnumber males on some of the feeding pastures off Southern Yemen. An overall sex ratio of 56% females and 44% males is based on a total of 4,376 individuals collected over a period of seven years. The figures include sub-adults and adults.

Caldwell (1962b) found that in Baja California waters, over four sampling periods in which the number of landed turtles varied from 104 to 465, females comprised between 68 and 92% of the catch. Presumably these were taken on the feeding pastures and were sub-adults and adults.

Carr and Giovannoli (1957) examined two cargoes of green turtles caught on the feeding pastures off Nicaragua between February and April, and in one case there were 27 males and 66 females; in the second cargo were 105 males and 271 females. The sizes were not given, but all were probably sub-adults and adults.

Expert turtle fishermen in the Kingdom of Tonga have advised Hirth (MS) that females outnumber males in the feeding pastures off Tongatapu.

It is common to see more males than females, at least for part of the breeding season, off some of the major nesting beaches. Reasons for this are discussed in section 3.13.

4.12 Size composition

According to Caldwell and Caldwell (1969), the "scarcity of records of small turtles seen in the ocean as compared with adult or sub-adult individuals is a most intriguing and puzzling circumstance. While the apparent rarity may result from not looking in the proper places, it may be that the lack of numbers is real. Considering the high mortality of the very young, the rapid growth of those that survive, and long life after reaching maturity, it is quite possible for the population to consist mostly of larger turtles".

Data relative to the sizes of nesting females are given in Fig. 6. Sizes of grazing males and females in the Gulf of Aden are given in Table IX.

4.2 Abundance and density (of population)

4.21 Average abundance

It is estimated that about 10,000 females make up the entire population nesting on the Sarawak Turtle Islands (Banks, 1937; Parsons, 1962; Honegger, 1968). Schulz (1969) estimates that there are about 2,500 females in the entire Surinam population. Carr (1969b) calculates that about 6,000 females nest annually at Tortuguero. Hirth and Carr (1970) estimate that less than 1,000 females nest annually on Aldabra. Dr. Bustard estimates the total breeding female population of the three common species (green, flatback and loggerhead) in Queensland waters to be not less than 75,000 (Anon, 1970g).

Relative sizes of other nesting populations can be ascertained by referring to references given in Table II.

Cromie (1966) states that green turtles represent about 20% of all turtles found throughout the warm seas of the world.

4.22 Changes in abundance (see section 5.4 for a discussion of the significant decreases in sizes of turtle populations)

4.3 Natality and recruitment

4.31 Reproduction rates

Details of egg production are provided in sections 3.16, 3.17 and 3.2. Some of the important aspects of reproduction pertaining to population studies are (1) a typical, adult female produces about 550 eggs each reproductive season and this usually is every two or three years, (2) some females may not retain reproductive capacity throughout life, (3) at some major rookeries about half the eggs laid do not hatch, and (4) on high density nesting beaches some incubating eggs are destroyed by turtles nesting later.

4.32 Factors affecting reproduction: see sections 3 and 4.5

4.33 Recruitment (Some factors determining recruitment such as growth and seasonal movements are discussed in sections 3.4 and 3.5)

4.4 Mortality and morbidity

4.41 Mortality rates: see section 3.22 and Fig. 9

4.42 Factors causing or affecting mortality (Predation on eggs, young and adults has been

discussed in sections 3.17, 3.22 and 3.34. The direct and indirect effects of fishing are discussed in section 5)

4.43 Factors affecting morbidity (Some parasites are listed in section 3.35 and chelonitoxication is discussed in section 3.44)

4.5 Dynamics of populations (as a whole)

Bustard and Tognetti (1969) have produced a model to show how nest destruction is dependent on population density and how this provides a mechanism to regulate population size (see Fig. 15). The mechanism tends to keep a population within certain limits. They state that "at a low population density its effects are negligible; however, if a population increased greatly, it would not stay at the new level due to this mechanism, which tends to restore the population to its original level." They also postulate that the Barrier Reef region of Australia may be the last place where natural regulation of population size by the mechanism of density-dependent nest destruction can still be observed today. This is because on many other nesting beaches the species has been seriously overexploited and the population density is below the level at which nest destruction by turtles would operate as a regulatory mechanism.

Bustard and Tognetti's model would also seem to be operational for such sites as the Sarawak Turtle Islands where many eggs, if not dug by man, would be destroyed by turtles nesting later.

4.6 The population in the community and ecosystem

Green turtles are large, egg-laying, marine reptiles well adapted to their aquatic habitat, but who periodically crawl onto dry land to lay their eggs. At such times, when on their nesting beach, they may be the dominant nocturnal vertebrate of the strand association. Their crawling and digging activities at least temporarily affect the beach topography and their eggs and hatchlings are a source of food for a variety of predators (see sections 3.21 and 3.22).

The distribution of adult green turtles in the littoral and sublittoral zones of tropical seas is directly related to their nesting beaches, feeding pastures and perhaps ocean currents. Long-range biennial or triennial nesting remigrations across deep water are typical for at least some members of some populations, i.e., the population of green turtles in any given region may include two components, a migratory group, and a group that remains in the area year-round and nests on the nearest optimal beach (see section 3.5).

The relationship of green turtles with competitors in the "turtle grass community" is discussed in section 3.42. Most adults occupy the second trophic level in a simple predator food chain, viz., plant-turtle. Hatchlings and small juveniles are chiefly carnivorous and hence occupy at least the third trophic level in a predator food chain, viz., green plant-herbivore-hatchling.

The green turtle occupies a broad ecological niche. This is partly due to the lack of strong interspecific competition.

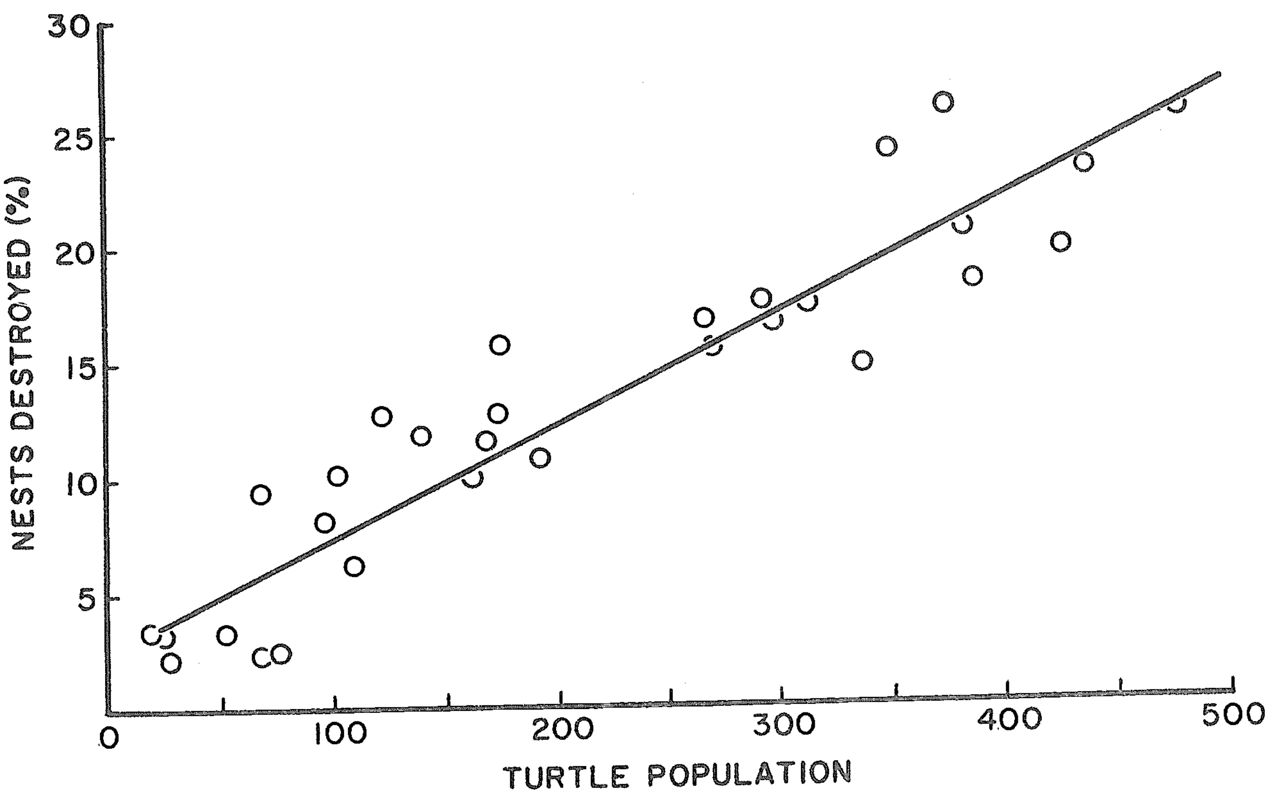

Fig. 15 Model showing correlation of nest destruction with size of turtle population (from Bustard and Tognetti, 1969; Copyright, 1969, by the American Association for the Advancement of Science)

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gears and methods

Indigenous methods of turtle fishing include diving for them and using harpoons, spearguns, traps, seines, suckerfish and decoys.

Green turtles are usually caught on their feeding pastures by using nets and seines. Carr and Caldwell (1956) describe how turtle fishermen seeking juvenile and sub-adult individuals on the grass pastures off the Gulf coast of Florida use tangle nets from about 97 to 194 m long, 2.4 to 3 m deep, and with a 20.3 to 30.5 cm bar mesh.

Duncan (1944) describes how Cayman Islanders capture turtles with nets on the feeding pastures off Nicaragua, and Parsons (1962) further describes how turtlers on the Nicaraguan pastures "set their nets over marked rocks to which the turtles customarily retire at night and wait for them to become entangled in the nets when they surface to blow". Huxley (1962) gives a very brief account of turtling by the Cayman Islanders.

The beach seines used by the Yemeni in the Gulf of Aden to catch sub-adults and adults vary from about 97 to 388 m in length and are up to 12 m deep with a 10 to 46 cm mesh (Hirth and Carr, 1970). According to Tressler and Lemon (1951) the most popular form of gear for catching turtles is the gill net.

Vaea and Straatmans (1954) describe turtle netting on the pastures in the Tonga Islands as follows: "A fisherman, having located an area of seaweed between the small, uninhabited islands, drops his net in a straight line at right angle to the flowing current and returns home. After two days he goes back to retrieve his net and usually finds turtles of all sizes caught in the net. In a 50 by 12 ft net, as many as ten turtles can be expected and often more, depending upon the length and width of the net and the area where it is dropped".

Yonge (1930) has described how natives used to dive for sleeping turtles off the Great Barrier Reef. Some of the ways of fishing for turtles in the Trust Territory are described in the Anthropological Working Papers (1957).

Suckerfish or remora (Echeneis sp.) have been used to capture turtles in such widely scattered places as the South China Sea, northern Australia, east coast of Africa and the Caribbean. Parsons (1962) gives an excellent account of this extraordinary custom.

Scuba divers use spearguns to get green turtles of various sizes in such places as the Seychelles Islands, Caribbean Islands, and some South Pacific Islands.

Harpoons are widely used to capture both sexes when they congregate off the nesting grounds. McCarthy (1955) describes, in a popular way, how aboriginals harpoon turtles in the Gulf of Carpentaria.

Schmidt (1916) described how the fishermen in the Dutch West Indies used wooden decoys in the shape of a turtle, along with nets, to capture green turtles. Wooden decoys are still used in several areas of Central America. They are especially useful in attracting males.

On the nesting grounds adult females are simply "turned on their backs". This can be done by one man. No special equipment is needed to locate and dig up the eggs on the beaches, although a straight stick to probe for the eggs is useful.

Mechanized turtle hunting is becoming more widespread. Two companies operate in the feeding pastures off western Australia and the following account describes their methods (Anon, 1969c): "Each licensed freezer boat has several small 16-ft scooter catcher boats, powered by 40 hp outboard motors. These scooter boats operate within a one-mile radius of the mother freezer boat, in the relatively shallow water inside the offshore reefs, where the turtles graze on the brown and green algae of the rocky sea bed. When a turtle is located, it is harpooned from the scooter boats as it races through water from 3 to 8 ft deep. On attaining a full load of about 10 turtles, the scooter boats unload their catch on board the freezer boat for processing. Turtles are gutted, beheaded, washed, drained and blast frozen. Each carcass weighs about 120 lbs dressed. When the freezer boat attains a full load, usually about 300 turtles taken in about three days' fishing, it returns to port to unload its catch".

5.12 Boats: see preceding section

5.2 Fishing areas

5.21 General geographic distribution

Most green turtles are caught on their feeding pastures, in shallow water just off the nesting beaches, and on the nesting beaches (see section 2).

5.3 Fishing seasons

5.31 General pattern of seasons: see sections 2 and 6

5.32 Dates of beginning, peak and end of seasons: see section 6 and Table XI

TABLE XI

Current regulations regarding the harvesting of green turtles and their eggs

Location	Regulation
	Pacific Ocean and adjacent areas
Hawaiian Leewards	complete protection for all marine turtles and eggs (Anon, 1968b; Hendrickson, 1969; Laycock, 1970).
Midway Island	protection for turtles less than 60 cm in carapace length.
Trust Territory of the Pacific	full protection for turtles and eggs on shore; and in the water for turtles with carapace length less than 61 cm (Wilson, 1969).
Kingdom of Tonga	following regulations now waiting approval by Government: complete year-around protection for eggs and for turtles with carapace length more than 87.5 cm; protection for all turtles of all sizes from 1 November to 28 February; ban on the sale or export of any turtle shell greater than 87.5 cm; complete protection for the leatherback of all sizes at all times.
Fiji Islands	same regulations as for Tonga, awaiting Government approval.
Rose Atoll, American Samoa	complete protection for turtles and eggs.
Malaysia	complete protection for nesting turtles; Government controls harvesting of eggs (about one million annually); March is closed season for eggs in Sabah (Harrisson 1950-1969; Hendrickson, 1958; de Silva, 1968, 1969b).
Queensland, Australia	full protection for all marine turtles and eggs (Bustard, 1969d).
	Atlantic Ocean and adjacent areas
Mexico	full protection for eggs; permit required to take turtles during open season; on Pacific coast closed season generally extends from 1 June through 31 October; on Gulf coast closed season extends from 1 May through 31 August.
Costa Rica	adults and eggs fully protected on nesting beaches; and protection for turtles within 4.8 km of nesting beaches (but harpooners can operate beyond this limit).
Panama	full protection for the green turtle (Myers, 1970).
Surinam	complete protection for nesting turtles and eggs on some of the major nesting beaches (see text).
French Guiana	protection for adults and eggs during May, June, July (Anon 1969i; Pritchard, 1969).
Trinidad and Tobago	protection for turtles and eggs from 1 June through 30 September.
Ascension Island	full protection for turtles and eggs.
	Indian Ocean and adjacent areas
British Indian Ocean Territory and Seychelles Islands	complete protection for turtles and eggs (but see text).

5.33 Variation in date or duration of season: see Tables II, III and section 6

5.4 Fishing operations and results

Of the seven species of marine turtles, the green turtle is of the greatest economic value to man. Its flesh, eggs, and "calipee" (= cartilage used to make soup) have been eaten for centuries. Now the growing market for its skin and oil, coupled with the even greater need for animal protein especially in the tropics, places this reptile in an especially important but precarious position. Carr (1952) called the green turtle "the most valuable reptile in the world."

The numbers of turtles caught on the feeding pastures as well as the numbers of females taken from the nesting beaches have declined rapidly in the current century. Parsons (1962) provides a comprehensive cultural and historical survey of man's attitudes toward the flesh and eggs of the green turtle.

In some countries bordering the South China Sea, eggs rather than turtles are harvested. Banks (1937) reported that the Sarawak Turtle Islands yielded 2,119,912 eggs in 1927 and these had a value of U.S. $23,000. Of these, 70% were consumed or sold locally. In 1935, 98% of the 924,000 eggs collected (value U.S. $7,769) were consumed locally.

Harrisson (1962b, 1962d, 1965a, 1967b) has documented the decline of green turtles in Malaysia through an analysis of egg-harvest records. He points out that in the thirties a year with over two million eggs was commonplace, while in the early and middle sixties a year with less than three-quarters of a million (only 99,307 in 1966) was commonplace. He speculates that the reasons for the decline to be both local (i.e., disturbance of nesting females; increased small boating activity off nesting beaches) and international (i.e., large steamers and mechanized fishing fleets in area; catching adults at sea).

During the peak months of nesting on Langawan, one of the Philippine "Turtle Islands", about 45,000 eggs are collected and sold each month (Domantay, 1952-53). The same number of eggs, or more, are harvested on at least two other islands in the group. Fisher, Simon and Vincent (1969) estimate that one million eggs are collected annually in the Philippines.

In recent years, two western Australia processing companies have undertaken commercial exploitation of the green turtle off the coast of western Australia (Anon, 1969c). The areas fished comprise the territorial waters extending along the coastline for approximately 160 km north from south latitude 23°10'. In 1968 and 1967, respectively, the export of processed turtle meat from western Australia was about 164,558 and 135,922 kg. The fishing season generally commences in June or July and terminates in September or October.

Parsons (1962) has documented the overexploitation and demise of green turtles in various parts of the world, specifically in Bermuda, Dry Tortugas, the Caribbean Sea and in the Indian Ocean. The decline of the green turtle population in the Seychelles has been commented on more recently by Honegger (1967), Gaymer (1968) and Hirth and Carr (1970). According to Acharji (1950), green turtles off Ceylon are netted between November and March, and the annual catch is around 1,000.

An estimate of the economics of the green turtle fishery in some areas of the western hemisphere is provided by Ingle and Smith (1949). Statistics show that about 2,000 turtles were caught annually in Costa Rica from about 1930 to 1948. Twenty-five men were engaged in the fishery in 1948. These men caught turtles on the nesting beaches between June and September. The value of sea turtles exported from Costa Rica over a 15-year period varied from $9,161 in 1937 to $900 in 1942.

Murphy (1925) reported that a turtle fishery was operated from time to time out of Pisco, Peru. Its existence today is unknown.

Caldwell (1963) gives a historical summary of the turtle fishery in Baja California. Harpooning is the most common method of taking turtles in that area and the fishery operates year-round. Hubbs (1960) also mentions the turtle fishery operating in that area. Townsend (1916) reported a catch of 162 green turtles in a single haul of a seine 90 m long in San Bartolome Bay in the Gulf of California on 11 April 1889. They were reported to nest in April and May.

The average annual harvest of C.m. mydas from the east coast of Mexico between 1963 and 1967 was approximately 225 t (R. Marquez, pers. comm.). The mean annual harvest of C.m. carrinegra off western Mexico between 1963 and 1967 was about 5,300 t (R. Marquez, pers. comm.).

The development and decline of the green turtle fishery in the Gulf of Mexico, Caribbean and British Honduras has been discussed by Ingle and Smith (1949), Westermann (1953), Carr (1954), Smith (1954), Caldwell and Carr (1957), Carr and Ingle (1959), and Neill and Allen (1959). Carr (1954) stated that "more than any other dietary factor, the green turtle supported the opening up of the Caribbean".

An indication of the former abundance of green turtles around the Bahamas and Cuba is given by Catesby (1743).

The commercial catch of turtles (almost all green) in Hawaii in 1969 was 4,625 kg (value U.S. $2,320). These figures should be considered minimal because many more are taken but not reported.

Between 1953 and 1967 up to 262 green turtles have been sold annually in Papeete, Tahiti.

The Fijian's fondness for green turtles is well-documented in archaeological excavations (Gifford, 1951).

Parsons (1962) estimated that between 15,000 and 20,000 green turtles are taken annually to supply commercial markets. Reese (1917) mentioned that in one year 15,000 were imported into England.

The catches of marine turtles have increased significantly in recent years (FAO, 1970). The reported catches of sea turtles of all species increased from 20,000 metric tons in 1964 to 36 and 33 thousand metric tons in 1967 and 1968, respectively. Whether these increases are real or due to better coverage in more recent years is unknown. Japan and Mexico together accounted for 95% of the landings (of all species) in 1968. The breakdown by species is not known, but greens ridleys and hawksbills probably account for most of the landings.

All the available evidence indicates that green turtle populations are slow to recover from overexploitation.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.11 Limitation or reduction of total catch: see Table XI and following sections

6.12 Protection of portions of population

There are striking differences among various countries regarding protection of green turtles. There are no regulations at all pertaining to their capture on the high seas. Current regulations, that were available to the author, are set out in Table XI. Various other recommendations and the philosophy behind some of the ordinances are discussed in the following regional sub-sections.

Pacific Ocean and adjacent areas

It should be noted that the new Tonga and Fiji resolutions (see Table XI) will provide protection for all eggs and for animals above a certain size rather than below a certain size. The philosophy behind these ordinances is geared to the belief than an adult turtle remains reproductively active for a considerable number of years and protection of adults and their eggs should in time produce an increase in the population. Turtle populations in Fiji and Tonga should be monitored after these new laws go into effect since the ordinances may serve as models for other areas in the South Pacific. (In Tonga and Fiji the carapace is measured along its arch; straight line measurement would place the legal size a few centimetres below 87.5 cm).

As far as is known, the eggs are generally eaten in Thailand, Indonesia, Burma, Borneo and the southern Philippine Islands; adults are preferred in New Guinea and Melanesia (Penyapol, 1958; Parsons, 1962; Harrisson, 1962d; Somadikarta, 1968; and Anon, 1969d).

Atlantic Ocean and adjacent areas

In September and October 1969, representatives from Costa Rica, Nicaragua and Panama met in San José and agreed to suspend all turtling for a period of three years after which reappraisal of the status of the resource would be made and appropriate international controls could be established (Anon, 1970a; Carr, 1970a). If successful, this will be the first significant international agreement on sea turtles.

About half of the big rookery at Tortuguero, Costa Rica will be enclosed in the new Costa Rica National Park (Anon, 1968c; Anon, 1970h).

Complete protection is provided for adults as well as for eggs on some of the major nesting beaches in Surinam (Pritchard, 1969). On other beaches in the country, adults and their eggs are protected only during certain seasons. The Galibi nesting grounds in Surinam were declared a nature reserve in 1969 (includes Eilanti, Baboensanti, Pruimenboom and Galibi beaches). Local Caribs, however, are allowed to take a certain quota of eggs each year.

Indian Ocean and adjacent areas

Legislation recently passed by the Seychelles and British Governments (August, 1968) provides complete protection for both sexes and eggs throughout the Seychelles Islands and the British Indian Ocean Territory. Today there are no big, concentrated nesting places in the Seychelles Islands, although in the last century Aldabra was one of the biggest green turtle nesting grounds in the world. The general ecology of Aldabra and its potential role as a site for a biological research station (in contrast to its proposed role as a military landing strip), have been discussed by Stoddart (1967, 1968a, 1968b) and Beamish (1970). Brief descriptions of the Aldabran rookery are provided by Abbott (1893), Keynes (1959) and Hartman (1967). As in other places where the green turtle exhibits pronounced migratory patterns, the Seychellois are concerned over the fate of their turtles which now receive full protection on Seychelles beaches but which migrate elsewhere to feed and apparently get no protection (Anon, 1970d). The same situation led recently to the Tripartite conference among Panama, Costa Rica and Nicaragua (see preceding section).

In and near the Malagasy Republic, instituted turtle reserves are located at Nosy Anambo, Nosy Iranja, Nosy Trozona, Nosy Ve, Chesterfield Island and Europa Island. On some other beaches in the Malagasy Republic it is forbidden to take sea turtles when they are laying.

In Southern Yemen, green turtle flesh is mainly a commodity for export. In view of a growing export trade and possibility of over-exploitation, the Government of Southern Yemen was advised to limit the annual catch to 1,000, of which not more than half were to be females; and, to provide complete protection for nesting females and eggs on the major rookeries in the eastern provinces (FAO, 1968). Whether or not these recommendations have been adopted by the Government remains unknown.

Although there are no marine turtle conservation laws in West Pakistan, the green turtle rookery at Hawke's Bay seems in no imminent danger because local religious customs forbid eating of turtle flesh and very few indigents eat turtle eggs.

In September, 1968, the new African Convention for Conservation of Nature and Natural Resources was signed by 38 heads of state or their representatives. All marine turtles are placed in "Class A" which is defined as follows: "Class A species shall be totally protected throughout the entire territory of the contracting states, and the hunting, killing, capture or collection of specimens shall be permitted only on the authorization in each case of the highest competent authority and only if required in the national interest or for scientific purposes". Curry-Lindahl (1969) describes the events leading up to this African conservation convention.

6.13 Current status of the resource and action programmes

The green turtle is currently listed as a "depleted species" in the I.U.C.N. Red Data Book (Honegger, 1968). Consequently, at least for the present time, the keeping of green turtles as pets should be discouraged (cf. Murphy, 1968). Chelonia mydas is listed as a "peripheral" species in the 1968 edition of Rare and Endangered Fish and Wildlife of the United States (Anon, 1968a), and is included on Ziswiler's (1967) list of the most gravely threatened animals.

The green turtle (and all other marine turtles) was mentioned repeatedly in conservation resolutions adopted at the Second International Congress of the World Wildlife Fund which met in London in November 1970.

Many pleas for the wise management and conservation of green turtles have been made. Some of the more recent are those of Anon (1959), Hillaby (1965), Pritchard (1966), Carr (1967b, 1969d, 1970b), Bertram and Bertram (1968), Dumont (1969), Harrisson (1969b), Honegger (1969) and Crowe (1970).

In 1933 Moorhouse emphasized that much has still to be learned about green turtles, especially the sex ratios in the nest, survival rates, where young spend their lives, and growth rates. Forty years later biologists still know very little about these four facets in the life of the green turtle, all of which are needed in order to establish rational management programmes.

Major action programmes recommended by a group of sea turtle conservationists meeting in Morges, Switzerland (10-13 March 1969) included (1) increased incubation and hatchling programmes, using proven techniques, (2) study and analysis of world exploitation patterns, (3) a broad information programme, (4) beach surveys where data are lacking, followed up by expert advice as required, and (5) establishment of special sanctuaries under scientific management. The recommendations received much publicity (for example, Anon, 1969h; Anon, 1970b; and Anon, 1970c).

It is this author's opinion that in addition to the recommendations given above, major research thrusts should be directed toward population dynamics, productivity and studies on the ontogeny of orientation.

The establishment of breeding sanctuaries is certainly one way to perpetuate the stocks. Ascension in the South Atlantic, Europa and Aldabra in the Southwest Indian Ocean, Rose Atoll in the South Pacific and French Frigate Shoal in the Hawaiian Archipelago are good examples of such breeding reserves.

A series of marine national parks could also be established in key places where marine turtles are especially abundant. Kenya, for example, has two marine parks and is considering a third (see Randall, 1969, for discussion of marine parks).

The problems manifest in green turtle management and conservation are indeed complex. Factors that must be considered include turtle biology; local customs and religions; demographic trends; economics; federal regulations; and, perhaps most important of all, international cooperation. The fact that fishing jurisdiction claimed by nations varies from about 5 km to 321 km complicates any rational plan for the management of any marine turtle.

6.14 Public education

Because education plays a large part in any conservation and management programme, there should be more pictorial accounts like Jacques Cousteau's three film loops on the reproductive biology and conservation of the green turtle (available from Oceanography Unlimited, Lodi, New Jersey) and more films like the excellent turtle conservation film produced in Sabah and shown on television around the world (Bill Burrad Television Co., Los Angeles, California).

"Solomon, the Sea Turtle" is a semi-documentary film which portrays the homing prowess of a green turtle (see Anon, 1969e).

6.2 Control or alteration of physical features of the environment

The encroachment of vegetation and the accumulation of debris on some nesting beaches has been mentioned in section 3.16.

A study of the physical parameters of good turtle pasture is needed (see sections 2.22 and 3.42).

Bustard and Greenham (1968) found that on the Heron Island beaches not all egg chambers dug are successful. Failures are caused by obstruction of the digging action of the turtle by large or thickly matted tree roots and by collapse of the egg chamber sides due to insufficient support of the sand.

6.3 Control or alteration of chemical features of the environment

According to laboratory experiments of Bustard and Greenham (1968), green turtle eggs are able to hatch in chloride concentrations very much greater than those occurring in the natural egg chamber. Chloride concentration is not, therefore, a limiting factor in incubation success except for those few nests which are laid below the spring high tide mark. Bustard and Greenham also declare that they have successfully incubated many turtle eggs in coral sand moistened only with distilled water.

6.4 Control or alteration of biological features of the environment

A variety of species management programmes are in existence (see section 6.12).

Hendrickson (1958, 1961) believes that exploitation of eggs has a much less adverse effect on turtle populations than slaughter of adult females and that the exploitation for eggs is more profitable in terms of human nutrition than is exploitation for flesh and fat. Hendrickson's strategy of harvesting turtle eggs rather than meat can be briefly summarized as follows: the adult female has a high reproductive potential and the species is adapted to sustain enormous losses at the very early stages of its life. The harvesting of eggs constitutes exploitation at a stage when the species is adapted to withstand such losses. The individuals which do survive to adulthood presumably remain reproductively active for a considerable number of years. If the average female experiences more than three breeding seasons in a lifetime, then the weight of protein available in the form of eggs would exceed the weight available in the form of flesh and fat. The elegance of Hendrickson's scheme, at least in Malaysia, revolves around the fact that it is also in harmony with local customs and religion.

Hendrickson and Alfred (1961) estimated that about two million eggs constituting something over 50 t of high grade protein were consumed each year in Malaysia and they also stated "preliminary studies have indicated that as little as 2 or 3% of the nests, handled properly, could probably provide sufficient recruitment to the wild populations to keep them at their present level, provided other circumstances remain unchanged".

Since in some areas of the tropics about half of the eggs which are laid do not hatch, it would be of immense value to devise a method of distinguishing fertile from non-fertile eggs. These non-fertile eggs could then be utilized for human consumption.

Carr (1967b) stated that after over a decade of research at Tortuguero, Costa Rica, more green turtles are nesting now than in previous years, chiefly because of the increased hatchling yield. At Tortuguero adults are taken for local consumption and eggs are seldom harvested.

Although little is known regarding the numbers of males in a natural population, it may be that some of the hunting pressure on females could be relieved by cropping surplus males.

6.5 Artificial stocking

More than 100,000 hatchling green turtles from Tortuguero have been distributed to 28 different localities in Central and South America, Mexico, West Indies, Bahamas, Florida and Texas by the Caribbean Conservation Corporation (Dr. Archie Carr, Technical Director) in hopes of replenishing turtle stocks. Most of the releases are on sites where green turtles formerly nested in abundance. Batches of hatchlings are released with the hope that they go back to the place released - drawn there by some kind of sensory imprinting to taste, smell or feel. To date there are no indications of definite success; however, at some release sites it appears that some of the hatchlings are staying on and establishing resident populations (Carr, 1967b). A pictorial account of the restocking programme in the Caribbean is given by Parsons (1962) and Marquez (1966). Restocking programmes in Florida have been discussed in a popular fashion by Stephens (1968).

The "Brotherhood of the Green Turtle" is a loosely knit group whose efforts to save the green turtle led to the founding of the Caribbean Conservation Corporation.

Turtle hatcheries also operate in Malaysia and Australia. Harrisson (1950-1969) describes the long established hatcheries on the Sarawak turtle islands. In 1968 more than 100,000 eggs were dug up and reburied in the Sabah hatchery. An egg hatchery has been in operation for several years in Australia (Bustard and Greenham, 1968).

The current practices are to release hatchlings either on the beach or in the water both in the daytime and at night. Some are reared for several days or weeks and then released in the sea just off the rookeries. This latter procedure reduces mortality from littoral predators. However, what effects holding hatchlings in captivity and then releasing them at sea have upon their natural behaviour patterns are unknown.

At the present time the best (and simplest) method of natural stocking is to provide protection for nesting females, eggs and hatchlings on the rookeries. If predation on eggs and/or hatchlings is high and cannot be controlled, and in those few places where nesting density is so high that late nesters destroy the nests of their predecessors, then the establishment of centralized egg hatcheries on the nesting beach is justified. Hatchlings produced in these hatcheries should be released as soon as possible after emerging on the surface. Although, as previously mentioned, the methods of releasing hatchlings are debatable, i.e., whether to release them on the beach and let them crawl to the sea, or to release them from boats offshore, thereby eliminating littoral predation, this author favours the former because it most nearly approximates the natural behaviour of the animal.

The transplanting of eggs or hatchlings outside their natural nesting areas should be discouraged until some evidence of success is obtained in the Caribbean restocking scheme.

7 TURTLE MARICULTURE

Green turtle ranching and farming are still in the pioneer stages of development. True turtle farming implies that the unit is completely independent of wildstock (turtles live and mate under controlled conditions and lay eggs on man-made beaches). In turtle ranching the unit is dependent upon wild populations for eggs and the turtles are kept in varying degrees of captivity (i.e., from free-living individuals in fenced-off pastures to complete containment in concrete pools). Most turtle biologists believe that turtle ranching, if attempted at all, should be only a temporary scheme, the reason being that natural populations will not withstand continual "parasitization" of its eggs. Carr (1969a) points out another deleterious effect of the premature spread of turtle mariculture and that is the rise of new markets and high prices before the volume production necessary to satisfy demands and relieve pressure on natural populations is achieved. Needless to say, the ultimate in turtle mariculture is farming - using proven techniques of agriculture and animal husbandry. Initial attempts at turtle aquaculture should be on a small scale and should be conducted only if scientific expertise is available.

Some of the factors which must be considered before initiating a turtle farm (or ranch) are the following: long-term financing, elimination of predators and competitors in enclosures and on nesting beaches, protection from pollutants and poachers, availability of veterinarians to advise on disease problems, year-round availability of natural food (in nature, green turtle hatchlings are chiefly carnivorous and adults are herbivorous), growth rates obtainable with commercial feed, water and sanitary requirements, optimum density, pollution abatement, transportation to processing plants, expertise on how to utilize all turtle products (flesh, oil, skin and shell) and facilities to conduct scientific experiments concomitantly with the commercial scheme.

Shelbourne (1970) describes some priorities as far as marine fish cultivation is concerned and the same would seem to apply to turtle culture. In addition to some of the factors mentioned above, he describes the provisions of "high quality" seed stock and physico-chemical requirements.

Iversen (1968) describes some of the advantages of mariculture including the control of predation and artificial selection for rapid growth, high fecundity and resistance to disease. He also discusses current techniques of milkfish and mullet culture and mentions the green turtle as a candidate for sea farming.

Some general principles of aquaculture along with some of the problems and a few selective fish models have been discussed by Bardach and Ryther (1968).

The feasibility of turtle ranching has been mentioned in a general way by Schroeder (1966). Ehrenfeld (1970) postulates that turtle ranching may have some promise if the sub-adults and adults can be induced to stay on natural pastures near a farm without being penned.

Mowbray (1965) reports that green turtles mate regularly in the Waikiki Aquarium and that eggs are dropped in the water. He believes that they would deposit their eggs on a suitable artificial beach if one was provided.

Parsons (1962) reports how young South American river turtles, Podocnemis expansa, have been transplanted into Lake Valencia in the Andean highlands and are growing and nesting there. They are also utilizing artificial nesting beaches that have been constructed on some of the islands of the lake.

Diamond-back terrapins have been reared successfully in the United States and methods used here may serve as guides for sea turtles. A brief model for terrapin ranching is given by Ingle and Smith (1949).

Pseudemys scripta elegans have been farmed for 17 years in the United States (Haga, 1970) and some of the methods developed in farming this species might be adapted to sea turtles.

Pinchot (1970) discusses the possibility of enriching the lagoons of atolls and raising various animal species therein. His ideas merit consideration and would be especially applicable in the South Pacific region.

It may even prove possible as well as economical to grow certain plants via hydroponics for captive turtles. Several large European and American zoos have employed these methods to produce green grass supplement for zoo animals. The zoo keepers believe that high nutrition grasses may also stimulate reproductive processes and thus increase fecundity.

Preliminary experiments in Sarawak indicate that the first six months are the most difficult for rearing hatchlings in captivity (Harrisson, 1956a).

Significant pilot attempts at rearing loggerhead turtles in captivity (and resulting growth rates) have been described by Uchida (1967).

A pilot turtle ranch has been established on Great Inagua Island in the Bahamas, under the auspices of the Caribbean Conservation Corporation. Here about 1,000 ha of turtle grass pasture have been walled in and hatchlings have grown up to 3.6 kg in two years on a diet of conch (Carr, 1967b).

Five small green turtle ranches are now in operation in Torres Strait, Australia under the direction of Dr. H.R. Bustard (Anon, 1970f; Bustard, MS).

A pilot turtle ranch (or farm) is also operating in Cuba. Details are lacking.

At the present time a large turtle farm (Mariculture, Ltd., with about 40,000 turtles of various sizes) is in operation on Grand Cayman, British West Indies. Initial reports indicate a high degree of success in some aspects of the operation. Popular accounts of Mariculture are provided by Gabler (1969), Anon (1969g) and Anon (1969j).

According to Scott (1970) there are several major economic obstacles to the development of marine aquaculture, including (1) the absence of a strong demand for the high cost products of aquaculture (except for luxuries or freshwater carp) in spite of the rising world population, and (2) the absence of property rights in natural waters and problems of international jurisdiction on the high seas.

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SYNOPSIS OF FISHERIES BIOLOGICAL DATA

This is one of a series of documents issued by FAO, CSIRO and USFWS concerning species and stocks of aquatic organisms of present or potential economic interest. The primary purpose of this series is to make existing information readily available to fishery scientists according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in this series will be useful to other scientists initiating investigations of the species concerned or of related ones, as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fisheries resources. They will be brought up to date from time to time as further information becomes available either as revisions of the entire document or their specific chapters.

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